ECOLOGY

VOL. 42 APRIL, 1961 No. 2

DISPERSAL IN THE RED FLOUR BEETLE *TRIBOLIUM CASTANEUM* (TENEBRIONIDAE)

ALFRED F. NAYLOR [1, 2]
Department of Zoology, University of Oklahoma, Norman

INTRODUCTION

The purposes here are to report on dispersal in the red flour beetle *Tribolium castaneum* Herbst studied by methods developed for the confused flour beetle *T. confusum* Duval and to compare the species with respect to the process.

Previously (Naylor 1959) imago dispersal of *Tribolium confusum* was studied in a laboratory environment containing several equivalent flour niche units. In single-sex or mixed-sex groups, females displayed more-uniform-than-random and males showed more-variable-than-random ("contagious") patterns of spatial distribution; the behavior patterns of both sexes were largely attributed to density-dependent olfactory stimulus. No particular significance was attached to the male pattern; it was taken as evidence that, as so often happens, male functions are genetic and decorative. All emphasis was laid on the population survival value of interactions among the egg layers whose mutual responses would tend to reduce progeny crowding and to promote maximal exploitation of environments.

This last point was made as part of a generalized interpretation. Animals with requirements similar to those of *Tribolium confusum,* it was said, should be expected to have behavioral adaptations acting through dispersal processes to regulate density. The principle argued is sufficiently important to have its limitations made clear by tests on several species.

Ecologically similar and congeneric though *T. confusum* and *T. castaneum* are, they may be not closely related. The close morphological comparability of *T. confusum* to the much larger *T. destructor* suggests that resemblances to *T. castaneum* are possibly superficial; *T. confusum* and T. *castaneum* certainly show strikingly dissimilar chromosomal phenomena at meiosis (Smith 1952). Placement of the 2 species in separate genera would probably not be the most flagrant split committed.

A more pertinent reason for studying dispersal in both *T. confusum* and *T. castaneum* lay in the differences between the species in male responses to odorous products from imagoes. *T. confusum* males are attracted by smells of both sexes of the same species (Naylor 1959) while *T. castaneum* males are repelled (Loconti and Roth 1953). The possibility could not be ignored, although it was not substantially realized, that female dispersal pattern would consequently be somehow different in mixed-sex groups of the 2 species.

In ecologically significant respects, dispersal in these species seems to be very similar. But the results of the work with *castaneum* are less conclusive in slightly disconcerting ways than with *T. confusum.*

MATERIALS AND METHODS

Animals from eggs collected during 2 days were segregated by sex in the pupal stage. After eclosion half the beetles of each sex were marked with spots of aluminum paint. Then a period of 2 weeks was allowed as a check on the permanence of the marks before unmarked animals were mixed with marked animals of the opposite sex. Other details of technique were the same as described in the *T. confusum* paper (Naylor 1959) which has illustrations of the apparatus used.

In descriptive studies of dispersal 200, 400 or 800 animals were put for 2 days into set-ups of what I call the 48-vial general environment or 48GE. This apparatus consists of a ring arrangement of the closely spaced vials. Each vial holds about one gram of flour when filled to the brim which is flush with a rough paper surface afford-

---

[1] Present address: Department of Genetics, McGill University, Montreal, P.Q., Canada.

[2] I wish to thank Gerald Braver and Arthur W. Ghent for their helpful suggestions for revising the original manuscript.

TABLE IA. Raw statistics from mixed-sex groups in the 48GE apparatus. Sex marked with paint spots indicated by "m"; unmarked by "u." Other symbols: % = percentage of total present found in flour; ID = index of dispersion; r_{xx}' = correlation of number in adjacent vials; r_{MF} = correlation of sexes within vials

Sex & Mark	Time Order	800 ANIMALS				400 ANIMALS				200 ANIMALS			
		%	ID	r_{xx}'	r_{mf}	%	ID	r_{xx}'	r_{mf}	%	ID	r_{xx}'	r_{mf}
u♂	1	74.9	60.1	.084		86.0	45.7	−.387		99.0	52.8	.458	
m♀		55.8	41.8	−.045		70.1	49.1	−.317		84.8	47.4	−.024	
Total		65.2	46.7	.002	−.111	78.1	43.3	−.393	−.082	92.0	51.2	.340	.018
u♂	3	91.1	51.3	−.179		83.4	83.3	.111		100	52.3	.198	
m♀		54.2	31.8	−.205		61.9	31.7	.232		88.7	30.1	−.113	
Total		72.3	40.7	−.155	−.081	75.3	58.8	.222	−.036	94.4	39.5	.047	−.067
u♂	5	60.7	48.1	.128		78.8	88.9	−.014		78.0	70.9	−.180	
m♀		32.8	63.4	.102		56.8	35.9	.067		70.8	33.6	.329	
Total		46.3	48.0	−.037	−.107	67.9	84.8	.034	.318	74.5	60.5	−.028	.142
u♂	14	84.0	61.2	−.047		91.2	46.3	.169		96.0	52.0	−.135	
m♀		70.3	46.0	.113		80.8	27.8	.050		95.1	27.4	.052	
Total		77.3	45.8	−.044	−.163	86.1	33.3	.239	−.126	95.6	40.1	.074	.013
u♂	16	83.4	47.1	−.001		89.8	53.4	.130		96.0	45.0	−.178	
m♀		69.0	31.5	.216		84.1	37.4	−.081		96.0	25.8	−.059	
Total		76.5	45.9	.081	.147	87.0	47.9	.000	.045	96.0	41.0	−.068	.162
u♂	18	66.9	42.7	.169		69.6	50.0	.087		87.8	62.5	−.179	
m♀		55.9	37.6	.065		66.3	37.8	−.033		81.8	55.9	.120	
Total		61.8	48.5	.066	.200	68.0	39.7	−.089	−.104	84.8	67.8	−.115	.145
u♂	26	74.8	88.1	−.287		85.9	45.2	−.107		87.0	40.4	−.023	
m♀		65.9	23.9	.222		88.8	30.4	.144		93.9	36.3	.067	
Total		70.4	53.4	−.233	−.101	87.3	38.9	.144	.032	90.4	47.6	−.026	.241
u♂	28	84.0	40.0	−.068		88.4	42.0	.046		97.0	52.0	.067	
m♀		72.3	29.4	−.083		82.7	32.8	−.121		87.6	44.3	−.185	
Total		78.1	37.2	−.147	.062	85.6	34.7	−.001	−.078	92.4	41.6	.006	−.141
u♂	30	86.7	34.0	.276		92.4	40.1	.032		95.9	57.1	−.054	
m♀		69.7	44.9	−.064		83.2	37.0	.057		94.7	28.4	.249	
Total		78.3	38.8	−.062	−.003	87.9	36.7	.280	−.052	95.3	46.1	−.064	.075
m♂	2	64.9	44.1	.283		88.3	41.3	−.051		85.6	57.5	−.015	
u♀		63.5	36.5	.116		78.4	48.9	.120		93.0	37.6	.286	
Total		64.2	41.0	.378	.019	80.9	35.3	−.028	−.215	89.3	54.2	.255	.155
m♂	4	65.5	41.2	−.074		88.3	54.2	−.039		91.5	43.5	.127	
u♀		54.7	51.0	.247		84.3	25.4	.101		92.0	30.1	−.058	
Total		60.0	40.8	.092	−.107	86.3	42.9	−.001	.074	91.8	32.3	.116	−.117
m♂	6	61.3	65.5	−.168		81.9	59.5	.194		75.8	73.6	.140	
u♀		45.9	40.2	.262		77.0	36.2	.140		69.0	37.4	−.004	
Total		53.4	49.5	.110	−.096	79.4	60.9	.349	.274	72.3	45.7	.101	−.188
m♂	13	53.9	67.3	.066		59.6	51.2	−.215		84.0	57.7	.126	
u♀		51.4	44.0	.217		72.4	31.3	.245		80.8	34.9	.016	
Total		52.6	60.0	.301	.082	66.0	46.9	−.008	.166	82.3	38.7	.072	−.161
m♂	15	83.3	39.4	.144		81.4	47.4	−.238		89.4	50.9	.202	
u♀		78.2	37.7	−.051		82.7	41.1	−.162		88.3	40.3	−.046	
Total		80.7	41.4	.039	.074	82.1	62.0	−.361	.403	88.8	43.1	.159	−.052
m♂	17	82.9	43.4	.072		92.7	48.4	.226		88.8	50.9	.079	
u♀		69.3	41.2	.105		84.6	37.2	.319		82.5	43.2	−.164	
Total		75.9	52.7	.165	.245	88.6	52.1	.337	.216	85.9	59.1	−.034	.258
m♂	25	71.9	52.3	.041		76.6	31.8	−.276		85.0	77.1	−.114	
u♀		73.2	35.1	.150		87.4	37.3	−.176		87.1	42.9	−.170	
Total		72.6	40.4	.163	−.078	82.0	34.6	−.204	−.002	86.1	73.7	−.134	.243
m♂	27	68.3	45.9	.008		81.6	44.4	−.002		84.0	45.8	−.048	
u♀		68.4	41.9	.127		85.2	29.3	−.108		77.0	39.4	−.130	
Total		68.3	49.2	−.301	.122	83.4	43.0	−.245	.172	80.5	46.2	−.091	.088
m♂	29	81.4	49.2	−.074		86.2	53.4	.011		90.9	55.1	−.143	
u♀		75.8	45.3	−.248		85.4	46.1	−.066		91.0	44.6	−.255	
Total		78.6	48.2	−.105	.018	87.1	54.0	−.218	.085	91.0	55.8	−.136	.122

Table IB. Mixed-sex summary statistics (means ± standard errors) and significance tests of summed indices of dispersion. The values of "t" are unit normal deviates, by Fisher's transformation, corresponding to the summed chi-squares. "P" is the probability of such a normal deviate; one-tailed tests are used on female data, but two-tailed tests on male and Total ID

Group	Sex	%	ID	r_{xx}'	r_{mf}	t	P
800	all ♂	74.4	51.2±3.08	.021±.036		1.80	.07
	all ♀	62.6	40.2±2.09	.069±.036		−3.09	.001
	Total	68.5	46.0±1.40	.017±.041	.007±.028	−0.42	.69
400	all ♂	83.5	51.5±3.33	−.018±.040		1.92	.054
	all ♀	78.5	36.3±1.60	.023±.039		−4.99	.00000
	Total	81.1	46.6±3.09	.003±.054	.061±.040	−0.16	.87
200	all ♂	89.5	55.4±2.39	.018±.040		3.54	.0004
	all ♀	86.3	37.7±1.86	−.005±.039		−4.26	.00001
	Total	88.0	49.0±2.50	.026±.031	.051±.034	0.88	.37

Table IIA. Raw statistics of single-sex observations. The first 9 lines of figures are male data and the last 9 are female data

Time Order	800 Animals			400 Animals			200 Animals		
	%	ID	r_{xx}'	%	ID	r_{xx}'	%	ID	r_{xx}'
10	70.8	106.8	−.137	76.5	114.7	−.078	71.9	70.8	.071
11	47.5	99.2	.150	43.0	90.3	−.271	60.3	112.8	−.241
12	43.5	70.6	−.273	61.5	92.2	.242	59.6	136.6	.018
22	66.4	101.6	−.259	80.1	70.3	−.105	81.5	172.4	−.050
23	69.7	122.1	.034	78.9	98.2	.069	64.8	116.2	.068
24	70.5	85.9	−.153	71.1	102.1	−.078	73.1	145.3	.151
34	75.4	120.6	−.018	77.9	146.6	−.067	78.4	152.9	−.091
35	75.7	173.2	−.062	75.0	142.8	.148	77.3	199.9	−.051
36	61.2	106.3	.026	65.1	114.1	.058	72.5	133.4	−.060
7	30.0	32.7	.055	46.1	32.7	.024	51.0	36.4	−.152
8	58.7	31.9	.096	54.7	36.6	.165	72.0	40.7	.057
9	57.5	24.2	−.122	72.6	29.7	−.236	78.5	48.8	−.135
19	45.6	44.3	−.105	56.5	26.7	−.382	61.9	31.4	.274
20	42.4	26.6	.167	49.8	43.9	.183	44.1	31.2	−.234
21	72.8	34.8	−.250	85.2	33.3	.181	78.1	33.0	.032
31	61.8	39.2	−.030	70.2	39.2	.069	71.2	28.9	.116
32	48.9	38.1	−.119	52.0	58.3	.079	70.2	54.0	.176
33	52.2	33.3	.212	56.6	40.2	.042	77.8	43.0	.108

Table IIB. Single-sex summary statistics and analyses

Group	Sex	%	ID	r_{xx}'	t	P
800	♂	64.6	109.6± 9.57	−.077±.047	15.3	.000
400	♂	69.9	108.0± 8.21	−.009±.051	15.0	.000
200	♂	71.0	137.9±12.34	−.021±.037	20.8	.000
800	♀	52.2	33.9± 2.06	−.011±.051	−4.37	.000
400	♀	60.4	37.9± 3.12	.014±.065	−2.96	.002
200	♀	67.2	38.6± 2.89	.027±.056	−2.71	.003

ing communication between vials. A 24 cm metal cover, 3.2 cm larger than the outside diameter of the ring of vials, confined the beetles. After the beetles had been released in the center of the ring and had wandered for 46 hours, vial-by-vial counts were made for comparison to a random distribution. Animals were reused several times.

Ability of the beetles to detect one another in flour was roughly evaluated in the device I named the "Preferendum Apparatus." From the surface this 10-vial device appears to be very similar to the 48GE, but a porous bolting cloth partition divides each flour holder into an upper and a lower compartment. The subcompartments have doors on the underside through which flour and beetles can be introduced. These cages were loaded with females and flour, males and flour, or just flour so that 5 of the 10 vials had different contents from their alternates on the ring. The contrasting loadings might then bias the choices of flour-filled upper compartments by beetles turned loose on the surface.

Results

Dispersal over a ring of 48 equivalent vials

The single series of observations discussed in this section encompasses the features of what were the first 3 experiments of the *T. confusum* studies. This new experimental design permits certain comparisons to be made that were not possible before. For these studies 2 sets of 3 groups of 40-day-old imagoes were constituted as follow:

Set	Group	Number and Method of Marking
I	1	400 unmarked males, 400 marked females.
I	2	200 unmarked males, 200 marked females.
I	3	100 unmarked males, 100 marked females.
II	4	400 marked males, 400 unmarked females.
II	5	200 marked males, 200 unmarked females.
II	6	100 marked males, 100 unmarked females.

The 2 sets were alternately introduced into three 48GE apparatuses and 3 observations of animal distribution among vials were made on each group. Then beetles from stock were added to groups in which slight mortality and unaccountable losses had occurred. After 3 observations on each group as a mixed-sex group, the animals were separated by sex and marked and unmarked beetles from like-sized groups were pooled. Female groups were then used for 3 successive observations and the males for 3. The entire procedure described in this paragraph was carried out 3 times.

Statistics of each observation are recorded in parts A and averages are summarized for each group in parts B of Tables I and II. Each distribution of beetles over vials yielded a value of Fisher's Index of Dispersion (ID). This is computed as the sum of the squared deviations from the mean vial content divided by the mean. If beetles distributed themselves randomly among vials, ID would have a Chi-square distribution with 47 degrees of freedom. Both tails of the Chi-square distribution are of interest. Significantly low values of ID indicate repulsion among animals; high values indicate either real aggregational tendencies or environmental heterogeneity. Independent ID's may be added and the sum tested by Fisher's normal approximation. Negative and positive values of the unit normal deviate ("t") have the same meanings, respectively, as low and high values of Chi-square.

Positive bias in the circular coefficient of correlation between numbers in adjacent vials (r_{xx}) would arise from regularities—for instance, those caused by physical gradients—in the succession of counts around the ring of vials. In mixed-sex observations the correlation between the sexes (r_{MF}) can be computed from vial pairings of male and female counts.

The percentage of beetles present actually found in the flour is recorded rather than the mean vial count given in the *T. confusum* tables. The earlier paper (Naylor 1959) discusses the theories of the other statistics more fully.

The first thing to consider in Tables I and II is that in mixed-sex or single-sex groups *T. castaneum* distributions are much the same as those of *T. confusum.* Female indices of dispersion almost always fall below 47; females were more evenly distributed than would be expected on a random basis. Male ID's, on the other hand, usually are greater than the expected 47; there can be little doubt that single-sex male groups aggregate, although mixed-sex males may be moving about essentially at random except for slight environmental irregularities. The summed ID, analyzed in parts B of the tables, yielded significant tests except for the males in mixed-sex groups. However, one-tailed tests were applied to female data and more conservative 2-tailed tests to male and "Total" (ignoring sex) data. The reason for the difference is that the work of Loconti and Roth (1953) indicates repulsion within both sexes; but I was skeptical that male distributions would be more-uniform-than-random and did not want to commit myself to that particular alternative hypothesis.

The next thing to investigate is the effect of group size on ID. Disconcertingly, it is weak if it exists at all. Analyses of variance were performed to compare the variabilities of ID within and between densities. Only F values need be given:

Mixed-Sex Groups, 2 and 51 Degrees of Freedom	
Males	0.66
Females	1.12
Totals (sex ignored)	0.42

Single-Sex Groups, 2 and 24 Degrees of Freedom	
Males	2.73
Females	0.86

None of these is significant. Still, one can point out that average mixed-sex "Total" ID and female single-sex ID fall into sequences hinting at decreases with increasing density.

Rather sound evidence that increasing density does affect beetle movements comes from consideration of percentages found in flour. Comparisons of average percentages in Tables IB or IIB or any 3 percentages on one line in IA or IIA indicate rather unambiguously that a beetle is more likely to be found in flour if it is in a smaller group.

The next question that will be considered is whether there is any evidence of interaction between the sexes. Since it can be seen in Table IB that the average correlations between the sexes (r_{MF}) are very close to zero (.007, .061 and .051 for, respectively, the 800, 400 and 200 mixed-sex groups) the answer would seem to be no.

The question can, however, be approached in another way. One can ask whether average ID is affected by presence and absence of the opposite sex. To answer this, 95% confidence limits were calculated for differences between mean indices of dispersion of like-sized groups of each sex under single-sex and mixed-sex conditions. The limits for the mean female ID in the 400 single-sex group minus the mean female ID in the 800 mixed-sex groups are —9.91 and 5.28; for females' 200 single-sex ID less 400 mixed-sex ID, —3.93 and 8.58. Since both these pairs of limits narrowly enclose zero difference, the presence of males in 50:50 ratio seems to have practically no effect on female spatial pattern.

Different results are obtained, however, when the converse type of analysis is applied to male indices of dispersion. For males, the difference as mean ID in the 400 single-sex group minus that in the 800 mixed-sex groups has the limits 37.3 and 76.4; for the difference between mean 200 single-sex male ID and 400 mixed-sex male ID the limits are 57.7 and 115.57. Thus, there can be little doubt that the presence of females had a definite, and possibly very large, effect in reducing the tendency of males to aggregate among themselves.

In calculating the confidence limits just discussed Student's t statistic was used in its usual form on the female data. But, because variances seemed quite heterogeneous, Welch's modified form of t was used in calculating limits for male data (Hald 1952).

At this point, particularly because the discussion will soon pass to results obtained in preferendum studies, it would be well to examine Tables I and II for possible evidence that environmental irregularities strongly influenced beetle dispersal. The correlation of numbers in adjacent vials (r_{xx}') are available for this purpose. The coefficients for female data have something of a positive bias which is a bit stronger than appears as first glance because such a statistic has an expected value of —.021 instead of zero when no correlation exists (Naylor 1959). It is doubtful that environmental heterogeneity greatly influenced females but any such variability could obscure real differences in female dispersal at different densities. From single-sex male circular correlations, on the other hand, one cannot gather the slightest evidence that the high male ID's are due to technique. Male tendencies are almost certainly really aggregational, *i.e.*, involve some sort of interaction which causes males to form clumps.

Studies in the preferendum apparatus

As in *T. confusum,* males in *T. castaneum* aggregate and females disperse rather uniformly. In the former species males are attracted to and females repelled by the smell of other animals. In *T. castaneum,* however, Loconti and Roth (1953) found that both sexes were repelled by products extracted from glands of large numbers of beetles. This observation, standing by itself, would lead one to expect both sexes to distribute themselves uniformly.

I thought it might be possible to reconcile the results of Loconti and Roth with those obtained in the 48GE device in terms of concentration levels of the odorous compounds. Under exposure to weak smell from live animals, beetle behavior might be different from that under exposure to intense smell from concentrated extracts. This possibility was explored with tests in the preferendum apparatus, but it was not borne out.

Three apparatuses were available for simultaneous use. In one, each of 5 subcompartments received 50 males plus flour and the alternates only flour; in another, each subcompartment received either 50 males plus flour or 50 females plus flour; in the 3rd, loadings were 50 females plus flour or just flour. The open upper compartments were filled with flour and single-sex groups of 100 were turned loose on the surface to wander for 2 days. These groups were moved from device to device during successive observations until each of the 3 female groups was exposed to each of the 3 test situations twice and the male groups 3 times. Buried animals were also interchanged between subcompartments from time to time.

Let us assume that imagoes do not respond to smell, which is our null hypothesis. Interactions among females by means other than smell would tend to conserve this hypothesis by reducing distributional variability; in statistical terms the error of the first kind would be less than rejection probability. Male variability, however, would increase the probability of erroneous rejection. For the latter reason, 3 additional male observations were taken for the purposes of a weak test. Animals were reused, but group trials are independent under the terms of the null hypothesis which has the specific form that entry into flour holders of 2 available types depends on a binomial distribution with parameter ½.

Results are summarized and tested for significance in 2 ways in Table III. Pooled sums analyses treat the choice made by each animal at the time of entry into flour as a datum. In the other type of analysis a datum was the choice of compartment type made by the majority of beetles which entered flour. Either way, the same null hypothesis, biologically speaking, was tested. The majorities test is always over conservative; the pooled sums test is not conservative enough for male data.

TABLE III. Summary of Preferendum Studies

Contents of Subcompartments	♂♂	—	♀♀	♂♂	♀♀	—
Pooled male sums	177	243	126	117	175	219
P of male sums	.002		.61		.03	
Trials chosen by majority of males	2	7	5 *	2	1	8
P of male majorities	.18		.45		.04	
Pooled female sums	125	200	176	162	126	225
P of female sums	.00000		.48		.00000	
Trials chosen by majority of females	0	6	3	3	0	6
P of female majorities	.03		1.00		.03	

* Data for 2 trials lost by misrecording.

Both analyses of female responses make it evident that they were repelled by the smell of buried animals because they tended to choose vials with empty subcompartments in preference to those in which either males or females were buried. Neither sex markedly distinguished vials in the males vs. females choice. Males were obviously somewhat repelled by the smell of buried females.

Unfortunately, the reaction of free males to buried males is a little uncertain. The pooled sums test is significant but the majority choices test is not. However, in one of the two trials in which more free males chose compartments over buried males than over fresh flour the majority was 22 and the minority 21. Furthermore, if it is granted that males are repelled by females, then it must be admitted that this repulsion did not bias counts of free males found in male-loaded vials upward in the 2-sex situation.

The results simply confirm, and are not a complication on, those obtained by Loconti and Roth. Even when odor is not intense, *T. castaneum* imagoes of both sexes are repelled by the smell of either sex in flour. This is probably the mechanism producing female uniformity of distribution. Male aggregation, however, must come about by some overriding mechanism.

DISCUSSION

Space will not be devoted to reviewing the many ways in which the results resemble those obtained with *Tribolium confusum.* Instead this section will attempt to grapple with the untidier aspects of these studies on *T. castaneum.* There are 3 troublesome items to discuss: (1) the apparent failure of index of dispersion to change with density; (2) the aggregational behavior of males in spite of repulsion by imago smell, which should produce uniform distributions; (3) the yes and no answer to the question whether interactions between the sexes have been detected.

With respect to the lack of marked dependence of ID on density, the problem is most perplexing when females, especially in single-sex groups, are considered. At every density observed female distribution was decidedly uniform. Uniform distribution at one density should, by any logical line of argument, guarantee more pronounced uniformity at higher density. It should be noted that the female single-sex data do not flatly contradict logic, for the mean indices of dispersion do decrease with increasing density. The differences are just neither statistically significant nor very impressive.

Several effects may combine to obscure density trends in female ID. The evidence of correlations between adjacent vials suggests that females are rather sensitive to environmental irregularities. Also, notes made during observation mention quite spectacular asymmetrical surface aggregations. Technical variability and small sampling could, in part, account for lack of difference in female ID's.

The index of dispersion may not be the most efficient statistic on which to base comparisons. It is a very sensitive tester of the null hypothesis that a distribution is Poisson; but male and female distributions are not random. Comparison of distributions probably necessitates using the theory of the distributions actually observed. The desirability of choosing indices on grounds of the appropriate theory has been very well discussed in the context of human spatial distribution by Duncan and Duncan (1955).

Another explanation of relatively constant female ID may lie in the almost certainly real and substantial decrease with density of the proportion entering flour. Individual animals probably vary somewhat in their responses to the imaginal odor. Since at high density the females crowded into the flour would to some extent be ones which are less sensitive to the presence of others, less exact adjustments in vial densities would diminish the observed effect of more intense stimulus.

The explanations that have just been offered for lack of dependence of pattern on introduced densities must be accorded some weight. The available evidence does not allow a decision on their total adequacy.

In view of the behavior of the sexes in the preferendum apparatus, the near absence of correlation between sexes in mixed groups and male aggregation are unexpected. The 2 phenomena may be connected; but how is not readily apparent. If females and males flee each other in flour, which is the evidence of preferendum experiments on the species, then why are females not less likely to be found in vials where male aggregations have formed? If males flee sites where male smell is strong, by what mechanics are aggregations formed? What is it about the presence of females that reduces male aggregational tendencies? These questions can be more easily framed than given analytic answers. That the answers are connected somehow seems to be suggested by the following fact which was not previously mentioned. When single-sex male groups were introduced into either the 48GE or preferendum apparatus, flour levels in all vials had very markedly dropped below the vial rims after 2 days. Such packing almost invariably recurred despite the extra care taken, after it was first observed, to pack flour thoroughly in preparing set-ups for male observations. Flour levels neither rose nor fell in mixed-sex observations; females may have loosened the flour somewhat in single-sex groups. Just what significance these facts have in explaining male aggregation and lack of intersexual correlation cannot be said, but they are vaguely suggestive.

It is to be hoped that failures to resolve some perplexities arising from these observations do not distract attention from what is most important, namely the uniform female distributions. Their ecological importance has been discussed at enough length (Naylor 1959) and repetition will be avoided. Problems remain unsolved, but dispersal in *Tribolium castaneum* resembles, overall, that in *T. confusum*. The survival value of behavior patterns in the latter species was quite clear.

SUMMARY

Dispersal of *Tribolium castaneum* imagoes was studied by methods developed in work on *T. confusum* (Naylor 1959). The 2 species' behaviors are similar in the following respects: Females disperse more uniformly than random. Males aggregate. As density per unit volume of available flour increases, proportionately fewer imagoes enter flour. The female behavior can be explained by repulsion from imaginal smell in flour.

Some differences were observed in *T. castaneum*. For one, quality of spatial distribution is not markedly affected by density, but some rationalizations are tentatively offered. Unlike those of *T. confusum*, males of *T. castaneum*, are repelled by smell from imagoes; they nevertheless aggregate and no explanation can be given. Male aggregation is reduced by the presence of females, but no correlation between the sexes' distributions was observed.

Despite unresolved problems in *T. castaneum* behavior, it seems to resemble that of *T. confusum* in ecologically significant respects.

REFERENCES

Duncan, O. D., and Beverly Duncan. 1955. A Methodological Analysis of Segregation Indexes. Amer. Sociol. Rev. **20**: 210-217.

Hald, A. 1952. Statistical Theory with Engineering Applications. New York, John Wiley & Sons.

Loconti, J. D., and L. M. Roth. 1953. Composition of the Odorous Secretion of *Tribolium castaneum*. Ann. Ent. Soc. Amer. **46**: 281-289.

Naylor, A. F. 1959. An Experimental Analysis of Dispersal in the Flour Beetle, *Tribolium confusum*. Ecology **40**: 453-465.

Smith, S. G. 1952. The Evolution of Heterochromatin in the Genus *Tribolium*. (Tenebrionidae: Coleoptera). Chromosoma **4**: 585-610.

TURNOVER TIME AND PRODUCTION OF PLANKTONIC CRUSTACEA IN LIMED AND REFERENCE PORTION OF A BOG LAKE

RAYMOND G. STROSS,[1] JOHN C. NEESS AND A. D. HASLER
Department of Zoology, University of Wisconsin, Madison

INTRODUCTION

Bog lakes may be compared to engines which have operated on low-quality fuel and have, as a consequence, lost efficiency in the conversion of energy. Treatment of such lakes with hydrated lime provides at least a measure of temporary correction as inferred by the appearance of algal blooms (Waters 1957) and larger standing crops of zooplankton (Johnson and Hasler 1954, Waters and Ball 1957). The mechanisms by which alkalization augments production have been reviewed elsewhere (Stross and Hasler 1960).

The observed increases in standing crops of primary consumers following treatment is presumed to reflect an increase in production at this trophic level. If the assumption is correct, there is, as yet, no good evidence that the increase is transferred to the plankton consumer. Johnson and Hasler found no increase in production of rainbow trout, a secondary consumer in early life, in a lake treated with lime despite the observed increase in the standing crop of *Daphnia*, the chief source of food for the trout in the lake. They attributed a part of the failure to reduced utilization resulting from dilution of food following a lime-induced increase in depth of the aerobic zone of the lake. The susceptibility of trout to stress when competing with other members of the same species (Brown 1957) also may have been responsible for the failure of the trout to respond to the presumed increase in production of food. In view of the inconclusive circumstantial evidence, it became of interest to attempt a direct measurement of production at the level of primary consumers.

---

[1] Present address: Department of Zoology, University of Maryland, College Park, Maryland.

Measuring production of the planktonic Crustacea, the primary consumers, was made feasible with the help of 2 simplifications. It was assumed first, that an average standing crop was being replaced at a constant rate, and, second, that the rate of replacement of all species represented was approximately the rate of replacement of the dominant species. Because *Daphnia* dominated both portions of the lake, it was selected for this determination. The choice was facilitated by the fact that growth is proportional to the quantity of food available (Slobodkin 1954, 1959).

THE LAKE

The use of Peter-Paul Lake was appropriate for a comparative study because of the treated (Peter) and untreated portions (Paul). In 1951 Peter-Paul Lake (T45N, R8E, S36; Gogebic Co., Mich.) connected originally by a narrow, shallow channel, was separated with earth being used to fill the connection. Following the separation, Peter Lake (6 acres) received treatment with about 6.5 tons of hydrated lime over 3 years. The portion known as Paul Lake (3 acres) was preserved as a control.

Measurements of the physical and chemical characteristics of the water in the treated portion showed an increase in transparency, pH, and ions contributed by hydrated lime. During the 3-year period of the study the epilimnion and euphotic zone were about 50% deeper in the treated part. The zone inhabited by planktonic Crustacea was double that of the control as a result of an increase in depth of the aerobic layer. In the epilimnion pH was increased from 6.4 to 7.2. Alkalinity was increased by a factor of 3.0, calcium by 2.5 and magnesium by 6.0. There appeared to be no decline in the above values during 1955 and 1956, two years after treatment was discontinued. If regression in the chemical environment occurred, there was no evidence of it in the indices selected for measurement. A fuller description of morphometry and results of lime treatment are reported elsewhere (Stross and Hasler 1960).

METHODS

Collections of planktonic Crustacea and analysis of the samples were made in a conventional manner. Horizontal tows with the Clarke-Bumpus sampler were made over a circular course around the center of the lake and throughout the zone inhabited by the planktonic Crustacea at depth-intervals of one meter. Replicate samples were taken with each of mesh-sizes 2 and 10 bolting silk (0.37 and 0.16 mm i. m. d., respectively). Because the number of samples became cumbersome with this procedure, the method of Edmondson (1955) was employed during the final year and consisted of lowering and raising the sampler (#10 mesh attached) with a uniform motion while the boat circumscribed the course at uniform speed. Samples taken in the horizontal tows were strained from an average of 800-900 liters of water, and those in the composite sample (#10-mesh net), from 300-400 liters. Such collections were made from early May to mid-November, or during the ice-free period, and intensively from mid-June to late September. Samples were collected at time-intervals of 2 weeks in 1954, and of approximately 10 days in 1955. In 1956 the composite samples, which were used for determining turnover time, were collected each day and the horizontal tows, each week. All samples were preserved in an ethanol solution.

Numerical analysis consisted of counting the individuals of each species in three 1-ml aliquots which were taken from each of the 2 replicates. Weights were obtained from samples dried at 60°C and desiccated for 24 hours. Collections from the number-2-mesh nets were used because of their virtual freedom from contamination with rotifers and colonial algae.

Categorization of Daphnia according to size-age

In the enumeration procedure *Daphnia* were classified into 6 arbitrarily designated size categories, 3 postnatal and 3 embryonic groups, after the method of Slobodkin (1954). Separation of individuals into the postnatal categories was as follows: Adults included all individuals equal to or larger than the smallest individuals containing eggs or embryos in the brood pouch. The division of the 2 immature stages was, likewise, arbitrary, the minimum size of the intermediate or youthful stage being in accord with the minimum size of the adults under the assumption that the factors(s) governing growth of all postnatal instars had the same effect on all. The 3 embryonic stages were: (1) eggs fully swollen to the formation of fat droplets, (2) eggs showing cleavage to the formation of a pigmented eye-spot, and (3) embryos with eye spots until birth, or if the embryo had dropped from the brood pouch, until it resembled instar I. These stages were similar to those used by Edmondson (1955) except that stage I was of shorter duration than that given by Obreskove and Fraser

(1940). The portion of embryonic development occupied by each stage, as given for *D. magna* by Green (1956) for a wide range of temperature, was 27, 36 and 37% respectively. Visual inspection of a graph of the 3 embryonic categories disclosed no differential mortality. It was assumed therefore, that all uncleaved eggs were potential contributors to the populations of postnatal *Daphnia*. In other words, there was no evidence that eggs were inviable or that so called "egg-dropping" occurred.

RESULTS

Natural history of planktonic Crustacea populations

Only the census of the 3rd summer was satisfactory for calculations of production, but the information available for the previous 2 summers was useful in describing composition and phenology of species and annual trends in standing crops. Planktonic Crustacea in the untreated portion consisted mainly of *Daphnia pulex* and *Holopedium gibberum,* while in the treated portion the dominants were *Daphnia "longispina"*[2] and *Diaptomus*. Lesser members of the latter population included *Epischura* and *Diaphanosoma;* their occurrence was restricted to the summer period. *Cyclops* and, rarely, *Bosmina* were found in both portions.

The sequence in which the several species became the predominant members of the population was well established in both portions. When the ice departed the lakes in late April, the populations were composed entirely of copepods, and they occupied the warm water near the surface. In June the composition of the population diverged in the 2 portions. *Holopedium* became numerically dominant in the untreated portion and remained the most abundant member until July at which time the number of *Daphnia pulex* increased while the population of *Holopedium* declined. In the treated portion *Diaptomus,* the temporal counterpart of *Holopedium,* became clearly more numerous than *Cyclops* in June. It persisted as the most abundant member until July and then gave way to *Daphnia longispina*. The population of *Diaptomus* did not decline when *Daphnia* became dominant, as was true for *Holopedium,* but remained at approximately the same concentration. Each of the 2 species of *Daphnia* continued to dominate the respective portions for the remainder of the summer and early autumn. All Cladocera had become extremely rare, with one exception, by late December. Although the sequence of numerical dominance was fixed, the precise time dominancy changed hands was not. Nor did the time at which it occurred agree with the accumulation of heat as has been found to occur in other populations of planktonic Crustacea (Ward 1940). Whether or not competition between species played a part is unknown.

A competitive exclusion of *Cyclops* from most of the aerobic layer in the treated portion was suggested by the behavior of this species. The population was distributed near the surface in May; a short time later it was dispersed throughout the aerobic layer. But when *Daphnia* and *Diaptomus* became abundant, practically the entire population of *Cyclops* was found within a 2-meter zone located in the thermocline, the other 2 genera being dispersed above it. The concentration of dissolved oxygen in the strauum was 1.0 mg/l or less.

Standing crops

Seasonal trends in quantity of standing crops are shown in Figures 1 and 2. In the untreated portion the magnitude and time of occurrence of the pulses agreed rather well for 2 of the 3 years represented (Fig. 1). In the portion which had been treated with lime, the crops did not indicate such year-to-year stability. There was, in fact, a continuous decline in biomass during the 3-year period. Despite the decline, the average content of dried material in this portion for the 3-year period was somewhat larger per unit area of lake surface (Table I). The 14% greater amount did not compensate, however, for the 50% increase in depth of living space in the treated portion, and, therefore, the density of biomass was smaller than in the control. (The standing crops may be compared on an equal-volume basis if values from the treated portion are halved).

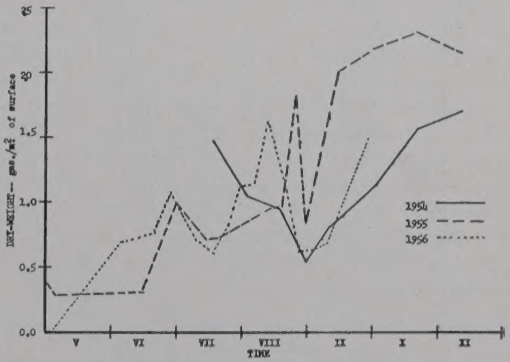

FIG. 1. Seasonal trend in standing biomass (dry weight) in the untreated portion of Peter-Paul Lake (#2-mesh met).

---

[2] See Brooks (1957) for reclassification of *Daphnia longispina* and exclusion of the species name from North America.

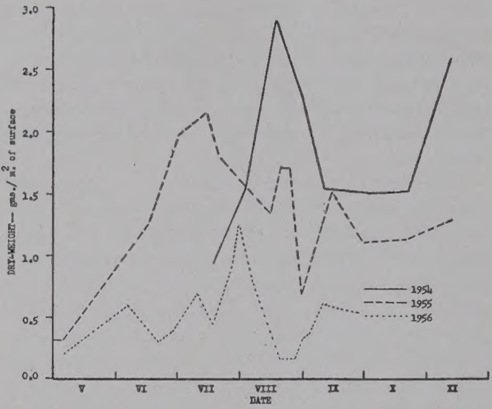

FIG. 2. Seasonal trend in standing biomass (dry weight) in the lime-treated portion (#2-mesh net).

Growth-form of Daphnia populations

When sampled each day for a period of 86 days, the 3 postnatal and a combined embryo category of *Daphnia* provided a comprehensible picture of population-growth. The population in the treated portion underwent one major oscillation and had begun a 2nd by the 86th day (Figure 3). In the control the population was involved in many fluctuations, but these were irregular and of smaller magnitude and duration (Figure 4).

TABLE I. Average standing biomass of planktonic Crustacea (#2-mesh net) in lime-treated and untreated portions of Peter-Paul Lake

Year	Period	g/m²	
		Treated	Untreated
1954.........	VII-15 to XI-15	3.16*	1.97
1955.........	V-1 to XI-15	2.23	2.04
1956.........	V-1 to X-1	0.87	1.51

* Some contamination by colonies of *Aphanizomenon.*

In the treated portion the population of *D. longispina* grew and declined in regular fashion (Fig. 3). Shortly after the period of sampling began, the population began increasing at a constant rate which persisted, with minor fluctuation, until early August. At this time it declined abruptly and at nearly the previous rate of increase. The decline continued until late August

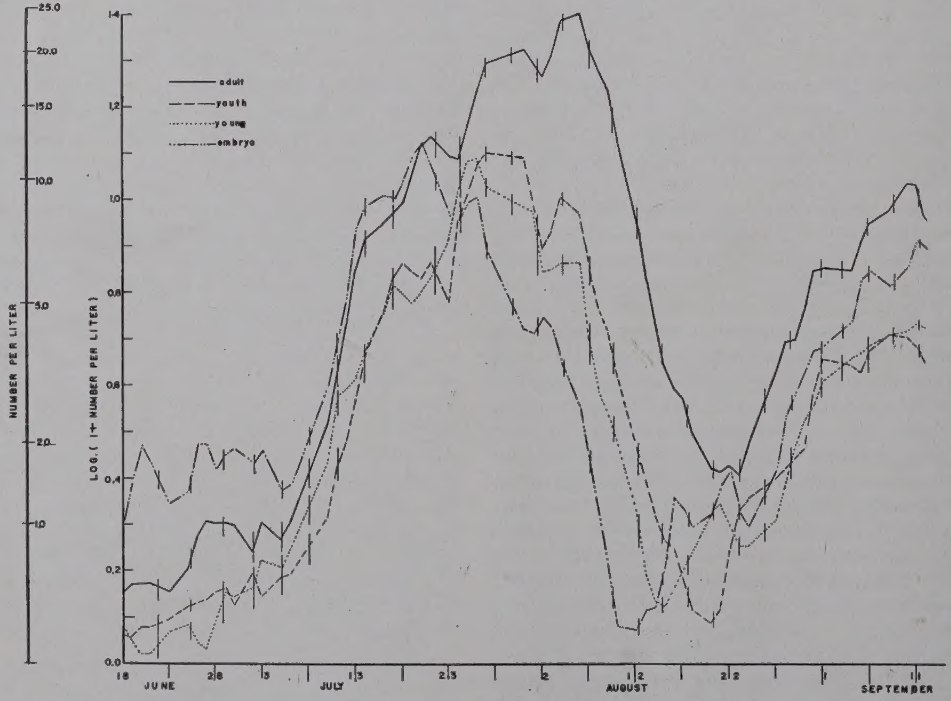

FIG. 3. Growth curve of 4 size categories of *Daphnia longispina* in the treated portion as determined by daily census with #10-mesh net during the summer of 1956. Vertical bars mark calculated interval required for development of embryos. (Curves smoothed by 3-point running mean technique).

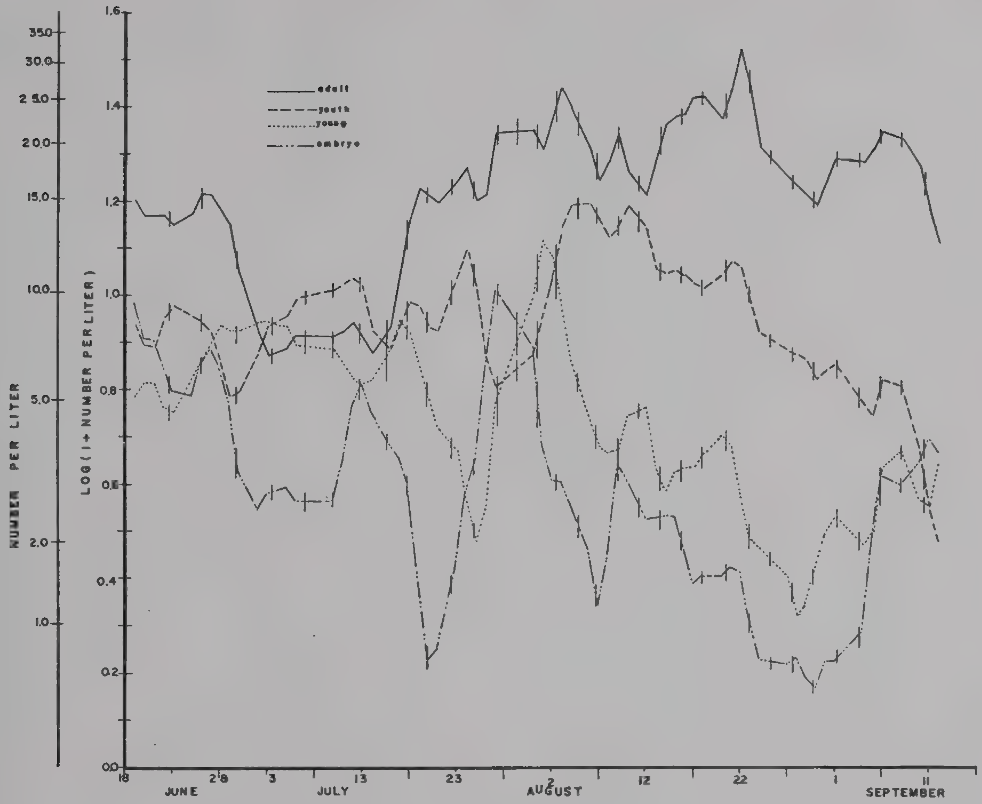

FIG. 4. Growth of 4 size-categories of *Daphnia pulex* in the untreated portion. (See Fig. 3 for further explanation).

when the population again began increasing and at a rate similar to that initially. A 2nd period of decline may have started at the time sampling stopped.

The adult category was most abundant of the 4 following the initial period of population development in late June. At this time there were more embryos than postnatal *Daphnia* in the population. The interchange in relative abundance of the 2 pre-adult categories during the summer is of interest. Normally, the juveniles, or youths, were more numerous, but with each period of renewed reproduction they were temporarily surpassed by the category of young animals. The repetitive nature of this relationship but confidence to the accuracy of estimated population-size. During the remainder of the period change in number of individuals in the 4 categories was uniform as is shown by the parallelism of the lines in Fig. 3; this was especially true as the population declined in August. It should be pointed out that with the decline of *Daphnia* in August there was a brief reappearance of *Holopedium,* which had disappeared after treatment began. Temporarily, it became as numerous as *Daphnia.*

In the untreated portion of the lake the population of *Daphnia pulex* did not grow at a constant rate for extended periods, although the period sampled did not include initial growth of the population. The adult category was always the most numerous of the 4, except for a short period of depression in early summer. Evidence of synchronous reproduction was interpreted from the uniformity of interval between successive peaks. Of the 6 major peaks, 4 lay wholly within the sampling period. Between the first and 2nd mode was an interval of 16 days, 14 days elapsed from 2nd to 3rd, and 13 days from 3rd to 4th. Because of the synchrony in reproduction, the growth of individuals through the size-age categories was normally visible although it became more obscure in the older groups.

An Estimate of Turnover Time

As mentioned previously, production of planktonic Crustacea in the 2 portions is compared by using the mean turnover time for *Daphnia* and the mean standing biomass of all Crustacea. As used here, "turnover time" is defined as the time required for a population of steady size to replace itself in numbers. For any interval of time, mean turnover time would be computed by multiplying the length of the interval by the (steady) standing crop given in numbers, and dividing the product by the total number of individuals recruited to the population during the interval. The populations under study were never steady in size for more than a short time so it was necessary to approximate turnover time by using mean standing crop instead of steady standing crop. Total recruitment to a population of steady size is equal to the number of deaths during any period. It includes all individuals added to the population regardless of whether they survive to the end of the period. Conversely, mortality is the sum of deaths during a period irrespective of birthdate. Neither was measured directly in the 2 populations of *Daphnia*. Total recruitment was determined from the number of individuals present in the broad pouch at the beginning of a period. Mortality during the period is simply the differences between the observed population size at the end of the period and that expected as a result of recruitment. The method is explained in detail.

To compute recruitment, an interval of time, Δt, was considered to be just equal to the time necessary for a brood of eggs to complete the embryonic development, *i.e.* Δt is the interval between ovulation of a given brood of eggs and the freeing of the resulting neonates from the brood-pouch. At any given time in a single-species population one may reasonably expect that Δt will be the same for all broods of eggs; it will vary in such a population from one period to another depending upon such variables as the nutritional state of the parthenogenetic females, or temperature. During an interval, Δt, changes in the numbers of individuals in each of the age-categories may be approximated from such relations as the following:

$$\Delta N_i = \beta_{i-1} N_{i-1} - \alpha_i N_i + \beta_i N_i \qquad \ldots(1)$$

where N_i is the number in the i^{th} age-category at the beginning of the interval, α_i is a coefficient of mortality for that category, considered to be characteristic of Δt, and β_{i-1} is a coefficient of recruitment (or growth) for the $i - 1^{st}$ category, also considered to be characteristic of Δt. In other words, during a Δt, each age-category recruits individuals as they grow into it from the next younger (or smaller) category and loses them through death and growth into the next older (larger) category. In what follows, all rates in these processes are considered to be linear functions of time (such that at time $t + \Delta t/2$ the changes that will have taken place between time t and time $t + \Delta t$ are half completed.)

Letting the subscript *1* refer to the age-category of neonates, *2* to the category of young, *3* to the category of youths, and *4*, to the category of adults (see above), we may write out the equations (1) individually as follows:

$$\Delta N_4 = \beta_3 N_3 - (\alpha_4 N_4) \qquad \ldots(2)$$
$$\Delta N_3 = \beta_2 N_2 - (\beta_3 N_3 + \alpha_3 N_3) \qquad \ldots(3)$$
$$\Delta N_2 = \beta_1 N_1 - (\beta_2 N_2 + \alpha_2 N_2) \qquad \ldots(4)$$
$$\Delta N_1 = N_o - (\beta_1 N_1 + \alpha_1 N_1) \qquad \ldots(5)$$

where N_o is the total number of eggs in brood-pouches at the beginning of the interval, all of which and no more than which will enter the neonate category during the subsequent interval, Δt. Solving (2) for $\beta_3 N_3$ and substituting in (3), we obtain:

$$\Delta N_3 = \beta_2 N_2 - (\alpha_3 N_3 + \alpha_4 N_4 + \Delta N_4) \qquad \ldots(6)$$

and continue in this way,

$$\Delta N_2 = \beta_1 N_1 - (\alpha_2 N_2 + \alpha_3 N_3 + \alpha_4 N_4 + \Delta N_3 + \Delta N_4) \qquad \ldots(7)$$
$$\Delta N_1 = N_o - (\alpha_1 N_1 + \alpha_2 N_2 + \alpha_3 N_3 + \alpha_4 N_4 + \Delta N_2 + \Delta N_3 + \Delta N_4) \qquad \ldots(8)$$

finally writing

$$N_o = \Sigma N_i + \Sigma \alpha_i N_i \qquad \ldots(9)$$

Inasmuch as the total recruitment to the population over any interval is equal to the change in size of the population over that interval plus the mortality during the interval, it follows that over each interval Δt, recruitment is equal to the number of eggs in brood-pouches as its beginning. If both sides of (9) are summed over all Δt for the entire season, the left-hand side will give recruitment for the entire season:

$$\Sigma_j N_{oj} = \Sigma_j (\Sigma_i \Delta N_i + \Sigma_i \alpha_i N_i)_j \qquad \ldots(10)$$

This is simply equal to the sum of the individuals in the brood pouch at the beginning of each of the successive and contiguous periods of length Δt filling the entire season.

Calculation of the embryonic period

The duration of embryonic development, Δt, because of its inconstancy over, say, an entire growing season, was approximated from the nutritional state of the mother (as indicated by average brood size), a value of Q_{10} for the species, and the average temperature of the zone inhabited by the population. Since the *Daphnia* in 1956 showed some tendency for crowding at intermediate depths, an average was taken of temperature of the zone inhabited by the populations. (The distribution of embryos, which were normally in the same proportion relative to the adults, indicated no special zone of high reproduction). Ingle *et al.* (1937) determined the duration of every instar in the life of *D. longispina* at 25°C at different levels of food supply. The durations given for starved animals were selected because of the comparable production of eggs by the adults in the lake and adults at that level of nutrition. Only the first 10 adult instars were used for determining the average development time. The average at 25°C was 49 hours but, under the range of water temperature during the study period, the values ranged from 62 to 88 hours. There were 30 such intervals during the sampling period, and their boundaries are indicated by vertical bars in Fig. 3.

Data comparable to Ingle's were not available for *D. pulex,* so it became necessary to calculate the average duration for instars of *D. pulex* from the amount of time required for the 2 species to reach the first adult instar under the same experimental conditions (Brown 1929). The development time for this species at 25°C was calculated to be 39 hours. The apparent higher rate of metabolism of *D. pulex,* in 20-degree water, and the slightly higher temperatures of the untreated portion, resulted in a faster overall rate of development, even though the time ranged from 51 to 92 hours. There were 33 periods for the population in the untreated portion (Fig. 4).

Turnover time and production

Total mortality, computed from equation (10), for the 86-day period was somewhat similar in the 2 populations of *Daphnia,* being 90 and 108 individuals/l in the treated and untreated portion, respectively. Table II gives the calculated mortality of each size-category, but, since the mortality coefficient during an interval Δt was considered to be a constant for all ages, the values reflect also the number of individuals contained in a category at the beginning of each interval.

TABLE II. Estimated mortality during the 86-day period distributed to the 4 size categories (number/l)

Portion	Embryo	Young	Youth	Adult	Total
Treated.....	13.0	13.0	17.0	45.0	88.0
Untreated...	15.0	17.0	24.0	52.0	108.0

The information necessary for calculating turnover time is included in Table III. It is seen that the *Daphnia* populations in the treated portion was being replaced at an interval of 2.1 weeks as compared to 4.6 weeks in the untreated portion. Both values would seem to be within the limits of an hypothetical maximum and minimum turnover for either of the species. They should not be considered to represent inherent rates for the species involved.

TABLE III. Comparison of statistics of the 2 *Daphnia* populations (number/l) and estimated turnover time

Turnover time (d) = $\frac{bc}{a}$	Treated Portion (*Daphnia longispina*)	Untreated Portion (*D. pulex*)
Initial population...............	1.1(−)	39.7(−)
Final population...............	19.4(+)	20.6(+)
Mortality..................	88.9(+)	108.3(+)
Total accumulation (a)..........	107.2	89.2
Mean standing population (b).....	18.1	33.4
Length of period (weeks) (c)......	12.3	12.3
Turnover time (weeks) (d)........	2.1	4.6

To determine production, the above rates were applied to the standing crops of the entire population of planktonic Crustacea existing in each portion. During the period May to October production was calculated to be 8.7 g/m² in the treated and 7.2 g/m² in the untreated portion. Thus, a faster turnover of the *Daphnia* resulted in the production of planktonic Crustacea being slightly greater in the treated portion and reversed the interpretation derived from comparison of the standing crops. Since the populations were mostly *Daphnia* for the period as a whole, variant turnover rates for the other species should have a minor influence on the overall value of production.

Prevalence of embryos and turnover-time

An obvious difference in the 2 populations of *Daphnia* was the much greater frequency of embryos in the treated portion. The population contained 2.2 times as many embryos and replaced itself 2.2 times as fast as the *Daphnia* in the control. The similarity of the 2 values, which was understandable, suggested that frequency of embryos may indicate turnover time. When examined it also seemed to reflect population-size inversely (Table IV). In the control, population-size and frequency of embryos were comparable for the 3-year period. On the other hand, the decline of the populations in the treated portion was matched, if not exactly, by an increase in frequency, thus implying that production was maintained despite the decline in standing crop. The compilations appearing in Table IV are based solely on collections with the number-2-mesh net since it was the only one used for all 3 years. The mean standing crops obtained with this net in 1956, although from a small number of samples, agree quite well with those obtained by daily sampling with the number-10-mesh net (Table III).

TABLE IV. Relationship of mean population size (SCm) of planktonic crustaceans and frequency of embryos in the *Daphnia* population in the 2 portions of Peter-Paul Lake

Year	Samples	TREATED		UNTREATED	
		SCm N/L	Embryo %	SCm N/L	Embryo %
1954	5	32.0	8.0	30.0	10.0
1955	9	26.0	31.0	28.0	10.0
1956	11	16.0	23.0	34.0	13.0

DISCUSSION AND CONCLUSIONS

The difference in turnover rates of the 2 populations of *Daphnia* in the 2 portions may be used to illustrate the weakness of using standing crops as indicators of production. On the other hand, the standing crop may be indicative of the amount of food being consumed because the larger population, as in the control portion, must expend more energy to maintain itself (metabolism) but, as a result, uses proportionately less energy for reproduction. Thus, the more productive population in the treated portion may not indicate, necessarily, a higher level of food intake. Because standing crop in this portion was the smaller of the 2, fewer calories may have been required to maintain it, with more of assimilated energy being available for reproduction. In *Daphnia* the time of turnover of the population should be inversely proportional to the fraction of energy expended in maintenance since the energy required for reproduction and maintenance are equivalent (Slobodkin 1959). If this relationship can be applied to all species, then the fastest turnover which is possible for a species under a given set of conditions should give the largest possible fraction of assimilated energy which can be captured by a succeeding trophic level, provided the efficiency of utilization is not affected by a large proportion of young (small) individuals in the population of prey.

Efficiency of utilization, however, can be modified by size and density of food. Brynildson (1958) has shown that rainbow trout perfer the larger *Daphnia,* and Johnson and Hasler (1954) found a positive correlation between density of *Daphnia* and growth of rainbow trout. In 1956 there were indications that trout production, based on growth rate in initially comparable populations, was greater in the untreated portion where the standing crop of *Daphnia* was larger, as were individuals, owing to the relationship of turnover time of a population to size of individual of indeterminate growth. In this particular link of the food chain there is probably an optimum turnover time which provides a maximum potential of utilization.

The faster turnover observed in this study is equivalent to the arbitrary value of 2 weeks used by Juday (1940) Lindeman (1941) and Dineen (1953) for the entire zooplankton. Since the planktonic Crustacea may be among the slowest of the zooplankton, a 2-week turnover time may be conservative, at least for the warmer months. It seems more important, however, to realize that turnover times in different lakes may vary considerably, enough so that arbitrary rates will not provide a sufficiently precise tool for the study of metabolism in aquatic communities.

Evidently, the treatment of bog lakes with hydrated lime results in changes in the species composition of planktonic Crustacea and the amount of biomass being produced. Morever, the new complex is unstable without continued treatment. An apparent stability of the population in the control may be ascertained from the rather consistent agreement between average standing crop and ratio of embryonic to postnatal *Daphnia.* Such was not the case in the portion previously treated with hydrated lime. Additional evidence of instability is provided by the transitory appearance of *Holopedium,* which was excluded as a result of treatment, following the "crash" of the *Daphnia* population. The disappearance of *Holopedium* as a result of addition of lime has occurred in other lakes (Brynildson 1958). Because of its intolerance to liming, the brief reentry of *Holopedium* suggests a regression of the treated portion to a former state. Thus, the continued application of lime seems warranted although there is no direct evidence of a decline in the gross changes wrought by previous treatment.

SUMMARY

Production of planktonic Crustacea on Peter-Paul Lake, Michigan, was used to determine whether application of hydrated lime enhances output of primary consumers. Production values were calculated from the average time required by the dominant crustacean, *Daphnia,* to replace its population and from the total biomass contained in a #2-mesh plankton net. Standing biomass was measured for 5 months beginning in May, and turnover time of *Daphnia* was measured for 86 days of summer.

Turnover times measured during the 3rd summer following the end of lime application were 2.1 weeks for *Daphnia longispina,* which occupied the treated portion, and 4.6 weeks for *D. pulex* in the control. Why one population replaced itself in a much shorter time was not determined.

Slightly more crustacean biomass was produced in the treated portion, according to calculations,

but only because of the apparently more rapid turnover of the *Daphnia* population. Standing biomass was roughly half that of the control and was lowest of 3 consecutive summers. Whether production decreased accordingly was debatable because an increase in the proportion of embryos in the *Daphnia* population could have signaled a compensatory shortening of turnover time.

A change in the age distribution of the *Daphnia* population and a brief reappearance of a species intolerant to lime treatment were indications of post-treatment regression. There appeared to be, however, no decline in the level of calcium, magnesium or bicarbonate, the major addition products of liming.

REFERENCES

Brown, L. A. 1929. The natural history of cladocerans in relation to temperature. II. Temperature coefficients for development. Amer. Nat. **63**: 346-352.

Brown, M. E. 1957. Experimental studies on growth. The Physiology of Fishes. M. E. Brown, Ed. Vol. 1: 361-400.

Brynildson, O. 1958. Ph.D. Dissertation. Univ. of Wisc. Library, Madison.

Dineen, C. F. 1953. An ecological study of a Minnesota pond. Amer. Midl. Nat. **50**: 349-376.

Edmondson, W. T. 1955. The seasonal life history of *Daphnia* in an arctic lake. Ecology **36**: 439-455.

Green, J. 1956. Growth, size and reproduction in Daphnia (Crustacea: Cladocera). Proc. Zool. Soc. Lond. **126**: 173-204.

Johnson, W. E. and A. D. Hasler. 1954. Rainbow trout production in dystrophic lakes. Jour. Wild. Mgmt. **18**: 113-134.

Juday, C. 1940. The annual energy budget of an inland lake. Ecology **21**: 438-450.

Ingle, L., T. R. Wood and A. M. Banta. 1937. A study of longevity, growth, reproduction and heart rate in *Daphnia longispina* as influenced by limitations of quantity of food. Jour. Expt. Zool. **76**: 325-352.

Lindeman, R. L. 1941. Seasonal food-cycle dynamics in a senescent lake. Amer. Midl. Nat. **26**: 636-673.

Obreshkove, V. and A. W. Fraser. 1940. Growth and differentiation of *Daphnia magna* eggs *in vitro*. Biol. Bull. **78**: 428-436.

Slobodkin, L. B. 1954. Population dynamics in *Daphnia obtusa* Kurz. Ecol. Monogr. **24**: 69-88.

———. 1959. Energetics in *Daphnia pulex* populations. Ecology **40**: 232-243.

Stross, R. G. and A. D. Hasler. 1960. Some lime induced changes in lake metabolism. Limnol. Oceanogr. **5**: 265-272.

Ward, E. B. 1940. A seasonal population study of pond Entomostraca in the Cincinnati region. Amer. Midl. Nat. **23**: 635-691.

Waters, T. F. 1957. The effects of lime application to acid bog lakes in northern Michigan. Trans. Amer. Fish. Soc. **86**: 329-344.

——— **and R. C. Ball.** 1957. Lime application to a soft-water, unproductive lake in northern Michigan. Jour. Wild. Mgmt. **21**: 385-391.

RESPIRATORY ENERGY LOSS AND ACTIVITY PATTERNS IN THE MEADOW VOLE, *MICROTUS PENNSYLVANICUS PENNSYLVANICUS*[1]

Richard G. Wiegert
Department of Zoology, University of Michigan

INTRODUCTION

In recent years ecologists have turned increasingly to the measurement of energy flow as a means of explaining the dynamics of both natural and laboratory populations of animals. Such studies require not only an estimate of the total energy consumption of a population, but also values for the different types of energy utilization such as maintenance, growth, and activity. The present study evaluates some of these factors for the meadow vole, *Microtus pennsylvanicus pennsylvanicus* (Ord). The methods of measurement of energy consumption also permitted the investigation of activity patterns, critical and lethal temperatures, and the effect of huddling on energy consumption. Unless otherwise designated, the metabolic terminology and definitions follow Brody (1945).

The determination of energy consumption in a given species is complicated by the fact that the basal metabolic rate decreases as the weight increases (Brody 1945, Kleiber 1947). Chambers and Summerson (1950) have reviewed the extensive literature describing the relationship between metabolic rate and body weight.

Most of the metabolic data on mammals have been obtained from fasting animals. Such data, however, give only a minimum estimate when used to calculate energy consumption by mammals in their natural environment. The present study was designed to evaluate the effect on the metabolic rate of providing food and water to animals and permitting activity.

Few data are available concerning the metabolic rate of *Microtus*. Hatfield (1939) measured the carbon dioxide production of individual voles for short periods of time. His data are equivalent to an oxygen consumption of 5 cc per gram of body weight per hour at an assumed respiratory quotient of 0.8 (Pearson 1947). Pearson (1947) and Morrison (1948) reported data on the oxygen consumption of *M. pennsylvanicus* measured over a 24-hour period, with the voles provided with food and water. The oxygen consumptions of the two voles used in this study ranged from 5.3 cc/gm hr to 2.3 cc/gm hr, with a mean value for the species of 3.2 cc/gm hr.

---

[1] Based on a thesis submitted in partial fulfillment of the requirements for the degree, Master of Science, from the department of Zoology, Michigan State University.

The use of variation in oxygen consumption as a measure of activity is well supported by the work of Hart (1952) and Fuhrman *et al.* (1946). Hart (1950) also showed that a given amount of activity produced the same increment of oxygen consumption over the basal rate regardless of the environmental temperature.

The literature contains conflicting statements about the 24-hour activity pattern of *Microtus.* Some observers have found the meadow vole active at all times (Hamilton 1937a, 1937b, Hatt 1930), while others report that the species is chiefly diurnal (Emlen *et al.* 1957, Seton 1909).

Laboratory investigators also differ with regard to the type of 24-hour activity pattern present in *Microtus* (Davis 1933, Hatfield 1940, Mann 1954, Morrison 1948). All of the above studies, however, demonstrated the presence of a 2-4 hour "short cycle" of activity in the voles.

The 24-hour activity patterns are quite labile (Calhoun 1945, Hatfield 1940). For this reason care must be used in applying results from the laboratory to field conditions. The present study will show the effect of captivity on activity patterns and offer support for the idea that temperature plays a large role in conditioning activity in the field.

I wish to thank D. W. Hayne under whose direction this investigation was begun. Valuable technical advice was given by E. P. Reineke and P. J. Clark. F. Golley assisted with the measurements of critical temperature. I am grateful for the helpful criticism received from M. Hensley and T. W. Porter of Michigan State University and F. C. Evans of the University of Michigan. The study was supported by funds from the Department of Zoology, Michigan State University.

METHODS AND MATERIALS

The respiratory energy loss of *Microtus* was measured by indirect calorimetry. The factor 4.825 cal/liter (Brody 1945) was used to convert oxygen consumption to energy values. Measurement of carbon dioxide production was not included in this study.

A modification of the apparatus of Maclagan and Sheahan (1950) was used (Figure 1). A 240 mm Pyrex desiccator was used as the animal chamber in the 24-hour runs and a quart Mason jar for the shorter, one-half hour, fasting runs. The apparatus is of the closed circuit type; the animal rebreathes air from which the carbon dioxide has been removed by soda lime placed in the bottom of the chamber. The apparatus was easily modified to permit the hourly measurement of oxygen consumption over a 24-hour period. Two units were used for the 24-hour runs and 6 for the fasting determinations. During the fasting runs, the animals were confined in small wire cages within the chambers.

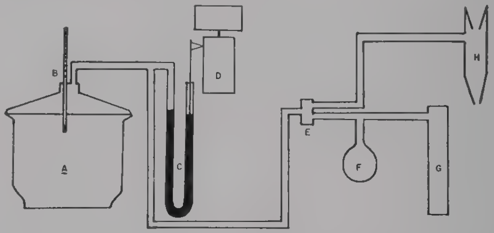

FIG 1. Diagram of apparatus used for non-fasting oxygen consumption determnations. 250 mm Pyrex desiccator (A), Thermometer (B), Mercury manometer (C), Kymograph (D), Two-way stopcock (E), Gas bag (F), Oxygen cylinder (G), Filter pump (H).

The volume of the system was determined by measuring the weight of distilled water that it could contain. The volume of the contents of the chambers was subtracted from this value. One gram of animal was assumed equal to one cc of volume. The temperature during a measurement period was never lower than 20°C nor higher than 30°. Corrections were made for changes in temperature and barometric pressure during the 24-hour runs.

For the 24-hour runs the animal was placed in the chamber (A) of Fig. 1. The lid of the desiccator was sealed with vaseline. With the stopcock (E) turned to the off position the gas bag (F) was filled from the oxygen cylinder (G). Then the stopcock (E) was turned to permit the filter pump (H) to draw a vacuum of approximately 200 mm as measured on the manometer (C). The stopcock (E) was then turned so that the vacuum was replaced with pure oxygen from the gas bag, then turned to the off position. This method of charging the apparatus is a modification of the original Maclagan-Sheahan apparatus devised by E. P. Reineke of Michigan State University. After replacing a 200 mm vacuum with pure oxygen the animal can draw a vacuum of approximately 160 mm of mercury before the partial pressure of oxygen in the system will be reduced to that of atmospheric air.

One hour was allowed for temperature equilibrium to be established and for the animal to become accustomed to the chamber. A reading was then taken of the level of mercury in each arm of the manometer tube and the difference between them recorded. This procedure prevented errors which would have been caused by irregularities in the tubing if readings were taken from zero on one side of the manometer only. As the pressure inside the chamber dropped, the scriber made a continuous spiral around and down the drum. The vertical distance between any 2 marks was then used to calculate the oxygen consumption for one hour.

For adult *Microtus* the apparatus had to be recharged after 12 hours. This took about 5 minutes so the hourly measurements of the latter half of a 24-hour run were slightly out of phase. Measurements were begun at various times of the day and night to avoid possible bias in the resultant activity patterns.

The voles used in this study were trapped on the campus of Michigan State University. The traps were set in late afternoon and the animals removed between 9:00 and 10:00 P.M. All voles which were to be fasted for 12 hours were placed in cages with water but no food and their metabolic rates measured the following morning.

RESULTS

Thermoneutrality and grouping experiments

The term "fasting metabolic rate" as used in this paper is defined as the rate of oxygen consumption of the fasting animal measured at the temperature of thermoneutrality and with activity restricted to a minimum. Since the activity of wild mammals can seldom be reduced to zero, "fasting metabolic rate" is probably a more accurate term than the more common "basal metabolic rate."

The author knowns of no published data on the critical temperature of the meadow vole. In order to provide an estimate of this value the fasting metabolic rates of 3 voles were measured at various ambient temperatures. Three Mason jar chambers were submerged in a small water bath. Measurements were made at 8 different temperatures. Small thermometers inside the chambers measured the environmental temperature. The length of a period of measurement was 20 minutes with one-half hour allowed for temperature equilibration.

The results are plotted in Figure 2 as the graph of oxygen consumption per mouse per hour against the ambient temperature. The data indicate that the lowest oxygen consumption occurred between 25 and 29°C. All subsequent metabolic determinations were made within this temperature range.

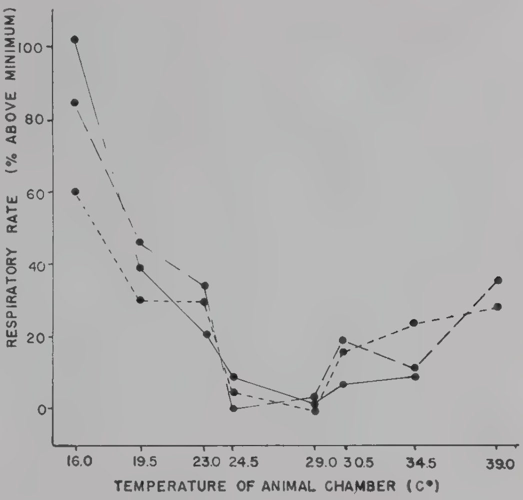

FIG. 2. Effect of temperature on the respiratory rate of three meadow voles, one female and two males.

As the environmental temperature was increased the voles exhibited signs of heat distress such as rapid breathing and flattening the body on the screen of the retaining cages. Between 34.5 and 39°C one animal died. The remaining 2 animals lived for only 40 minutes at the higher temperature. For this reason oxygen consumption at 39° was measured for only 10 minutes. Under the conditions of the experiment the lethal temperature for the meadow vole lies in the range of 34 to 39°C. Dice (1922) reported 36°C as the lethal temperature of the prairie vole *Microtus ochrogaster*.

The effect of grouping on oxygen consumption was investigated by measuring the fasting metabolic rate of several voles individually and then measuring the same animals as a group. Nine determinations of this type were made, the size of the groups varying from 3 to 5. The fasting metabolic rate, with one exception, was lowered when the animals were in a group. The non-parametric Wilcoxson test (Siegel 1956), showed the difference in rate of metabolism between the 2 treatments to be highly significant (two-tailed $P < 0.01$). In the single case where the oxygen consumption was lower when the voles were measured individually, the animals had not huddled together when grouped but had remained active throughout the measurement period.

Fasting metabolic rate

A total of 50 voles were used in the investigation of the relation of fasting oxygen consumption to body weight. Repeat observations were recorded on 12 of the animals. These replications were used to calculate a mean value for the individual vole. There was no selection for size.

Figure 3 is a double log plot of the data. The equation lines were fitted by the method of least squares (Brody 1945). The 95% confidence limits of b were calculated by the method of Snedecor (1956). The significance of the correlation coefficient ($r = + .505$) was high ($p < 0.01$). The value $b = 0.6424$ was significantly different from zero ($p < 0.01$). The fasting animals exhibited more extraneous activity and signs of distress as the duration of the fast increased.

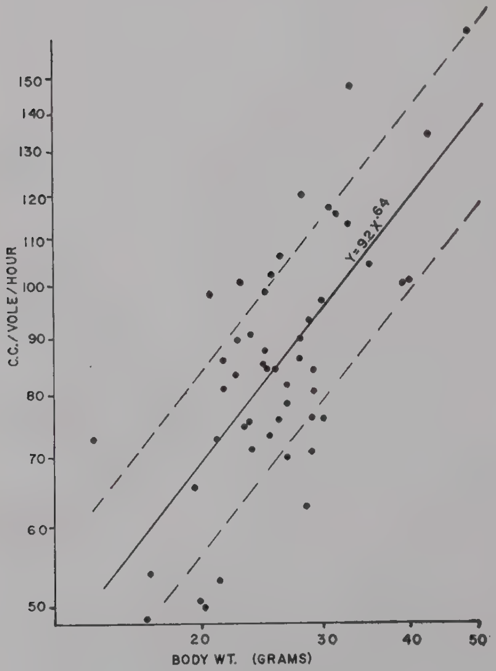

FIG. 3. Double log plot of fasting ozygen consumption of voles against body weight in grams. Dotted lines include one standard deviation either side of the regression line.

Metabolic rate with food and water available

The relation between oxygen consumption and body weight was investigated in voles provided with food and water and free to exhibit 'normal' activity patterns within the restrictions imposed by the size of the desiccator.

Figure 4 shows a double log plot of the mean hourly oxygen consumption against body weight. Because of the uneven distribution of the size classes in the field and the relatively small number of mice used, they were selected for weight. The solid circles on the graph represent data from 26 separate 24-hour determinations on 15 different voles. Weight changes between replications on the same individual ranged from 2 to 6 grams, with a mean of 2.8 grams. The increase in accuracy of estimation of the individual metabolic rate as a result of these replications outweighed the error introduced by the relatively small changes in weight. The 4 open circles represent 7 measurements on 4 laboratory born voles. These data were not used in calculating the regression line. They show good agreement with the predicted oxygen consumption of wild voles of the same weight.

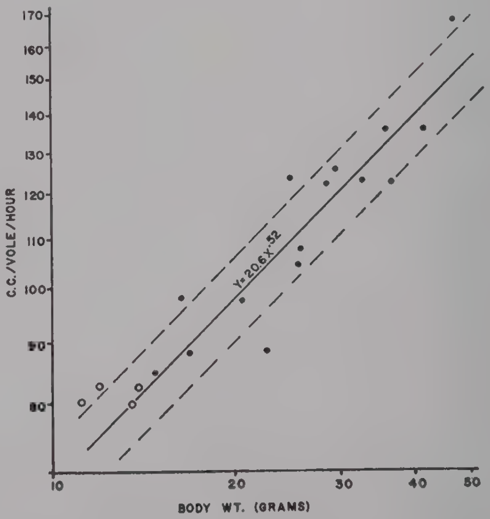

FIG. 4. Double log plot of non-fasting oxygen consumption of voles against body weight in grams. Data from laboratory bred voles (open circles) were not included in the calculation of the regression line. Dotted lines include one standard deviation either side of the regression line.

The data of Fig. 4 show much less scattering than do those of Fig. 3. The regression line equation of Fig. 4 was compared to that representing the fasting metabolic rate (Fig. 3) in order to test for differences in the slopes. The method of covariance analysis was used (Snedecor 1956). No significant difference could be shown to exist between the two values of b ($F < 1.0$). The great difference between the values of a for the 2 lines makes statistical comparison unnecessary. This higher rate of oxygen consumption in non-fasting animals was undoubtedly due to the specific dynamic action of the food consumed plus a higher average level of activity.

A measure of the diel variation in oxygen consumption is given by the maximum and minimum hourly rates which were recorded during the 24-hour runs. The mean values per weight class for maximum, minimum and mean hourly oxygen consumption per vole are shown in Figure 5. Superimposed on the curve of the mean oxygen consumption per weight class is the curve of the equation ($Y = 20.6\,X^{.52}$) which represents the relation of oxygen consumption to weight in nonfasting voles.

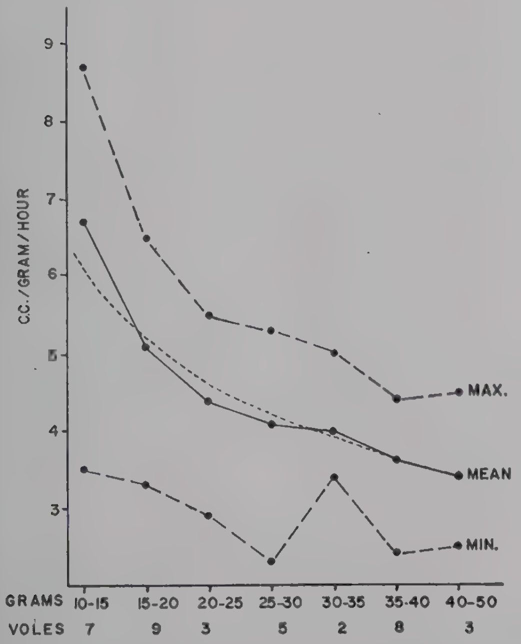

Fig. 5. Average maximum, average minimum, and average mean values for oxygen consumption over a 24-hour period for each weight class of voles. Number of individuals represented by each average indicated below weight class. Dotted line shows path of regression line $Y = 20.6\,X^{.52}$.

Daily activity based on variation in oxygen consumption

Data were obtained on the hourly rate of oxygen consumption from 29 uninterrupted 24-hour runs on 18 animals. These data were used to (1) determine whether the voles exhibited a nocturnal or diurnal activity pattern, (2) determine the duration of the "short activity cycle" if present, and (3) determine if a well defined 24-hour pattern of activity was present. Following the suggestion of Welsh (1938) the term 24-hour cycle was used to designate the correlation of activity with time of day.

The night/day ratio of oxygen consumption rates was used as a measure of nocturnal activity in each vole. Since all measurements were conducted with the apparatus placed in a window ledge, the only departure from photoperiod conditions present in the field was a reduction in light intensity. The data were recorded as the mean hourly rate of oxygen consumption at night divided by the mean hourly rate during the day. Replications on the same animals were averaged and a single value used for that individual. Using the Wilcoxson test (Siegel 1956) the difference between the night and day rates of oxygen consumption was highly significant ($p << 0.01$). The magnitude of the difference was, however, slight. The night/day ratio of rate of oxygen consumption for all animals was 1.09. The ratio for the laboratory voles was 1.25 and for wild voles 1.06. The latter value is identical with the ratio reported by Pearson (1947).

The length of the "short cycle" of activity was obtained from the 24-hour records. Consecutive hourly increases in oxygen consumption plus the corresponding consecutive hourly decreases were considered as a single fluctuation or "cycle." By this means each 24-hour record was divided into several periods. These are plotted in Figure 6 as percent frequency against duration. Where repeat runs were made on a single animal the mean number of periods of each duration for each animal was used. Two and 3 hour periods were the most frequent. The mean duration, *i.e.*, the total number of periods divided by the total number of hours during which measurements were made, was 3.6 hours. The mode was 3 hours. The data were analyzed by means of the non-parametric one-sample runs test (Siegel 1956). The two-tailed probability that such a distribution of runs was random was much less than 0.00006. Since the number of runs was far greater than would be expected under a random distribution, it is probable that systematic short-period cyclic fluctuations in activity are present (Siegel 1956).

To investigate the 24-hour activity pattern, the 24-hour oxygen consumption records of newly captured animals were compared with the records from animals held for some time in captivity. The oxygen consumption of each of 8 voles was measured for 24 hours on the day following capture. Six other voles were first held in captivity for periods ranging from 3 to 8 days. For analysis, the hourly readings were combined into 2-hour periods, following the suggestion of Morrison (1948) that this tends to show the presence of a 24-hour pattern of activity more clearly.

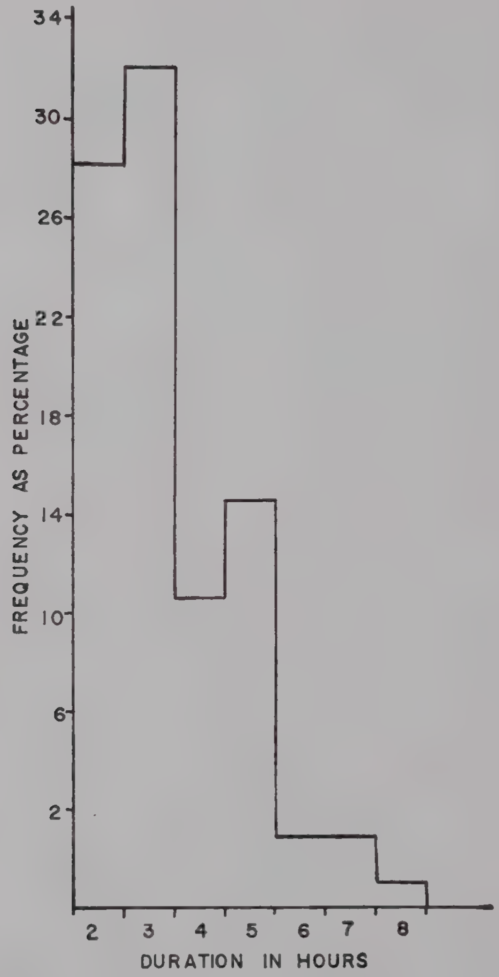

Fig. 6. Percentage frequency and duration of the short activity cycles.

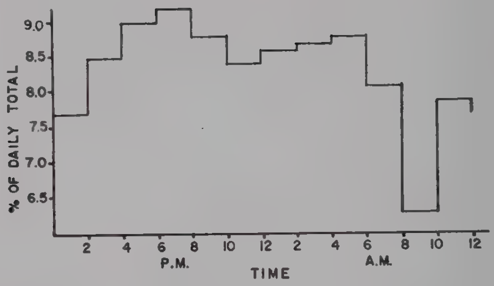

Fig. 7. Activity patterns of meadow voles 1 day after capture. Per cent of the total daily oxygen consumption for each two-hour period of the day. Mean measurements on eight voles.

The data from newly captured voles are plotted in Figure 7. Note the tendency for a bimodal pattern. The large drop in oxygen consumption between 8 AM and 10 AM was characteristic of all voles in this group. A graph of the data for animals held for some time in captivity showed no well defined bimodality. Both sets of data were tested by means of variance analyses. For voles which were measured the day following capture (Fig. 7) the effect of time of day on oxygen consumption was highly significant ($p < 0.01$). Voles held in captivity for several days before measurement did not show a significant effect of time of day on oxygen consumption ($p >> 0.05$). Both sets of data showed a significant difference between voles with regard to total oxygen consumption. Because of weight differences between voles, this was expected.

To investigate further the effect of captivity upon activity patterns, 24-hour oxygen consumption determinations were made on 2 voles during the first, 2nd, and 4th weeks following capture. These data were analyzed using a 3-way analysis of variance, 2 factors fixed and one random (Snedecor 1956). With the exception of the interaction of voles with weeks of captivity ($p < 0.01$) none of the tests was significant. Thus the total oxygen consumption varied according to the length of time in captivity but the direction of change was not the same in each vole. There was no correlation of oxygen consumption with time of day.

Discussion

Thermoneutrality and grouping

The results reported here suggest that the thermoneutral point for *Microtus pennsylvanicus* lies between 25 and 29°C. This is somewhat lower than the temperature of thermoneutrality in the laboratory white mouse, *Mus musculus,* in which Hart (1950) found the oxygen consumption lowest at 32°C.

The results of the oxygen consumption of grouped versus individually measured voles showed that combining animals in a group lowered the rate of oxygen consumption. Pearson (1947) reported that grouping tended to lower the oxygen consumption of the house mouse, *Mus musculus.* Most of his work was done at ambient temperatures below that of thermoneutrality. Some of his work however, showed that even at the temperature of thermoneutrality the mice had a lower oxygen consumption when measured in a group. Sealander (1952) found that huddling significantly raised the survival time of various species of the genus *Peromyscus* when the mice were exposed to temperatures below the lethal limit. It would appear from these results that one of the major effects of huddling is to reduce heat loss and thus to reduce oxygen consumption when the animals are measured at an ambient temperature below that of thermoneutrality. However, in the present study, huddling lowered the oxygen consumption even at the temperature of thermoneutrality. Since reduction of heat loss would not serve to reduce oxygen consumption at this temperature, it must be that the cessation of activity during huddling results in a considerably lower rate of metabolism. This mechanism has obvious value if it is desired to ascertain the true 'basal' rate of metabolism of the animal. Grouping of animals, however, is precluded in any study in which the oxygen consumption is to be correlated with weight, unless groups can be selected within which there is very little weight variation. The grouping experiment supports the idea that much of the scattering of points in Fig. 3 is due to differing levels of activity between individuals.

Fasting energy consumption

The fasting oxygen consumption of a vole of a given weight can be estimated by the formula:

(1) $Y = 9.2\,X^{.64}$ (Fig. 3)

The range of 95% confidence limits for b of equation (1) (0.46 and 0.83) indicates that b is not significantly different from the value of 0.73 reported by Brody (1945) or that of 0.75 reported by Kleiber (1947). This is particularly striking since Brody and Kleiber obtained their values of b from metabolic data of adults of many different species whereas the present study was confined to growing animals of a single species.

Brody (1945) has expressed the view that b should be considered accurate to only one decimal place. While this is logical in view of the usual experimental error involved in this type of measurement, it has the unfortunate effect of emphasizing the differences between the b values of Brody and Kleiber rather than their obvious similarities.

Using the caloric equivalent of oxygen (4.825) the energy consumption of the fasting meadow vole of a given weight can be approximated according to the relationship:

(2) $\text{Gram cal./day/vole} = 9.2\ (\text{weight in gms.})^{.64} \times 4.8 \times 24$

This includes the basal energy consumption measured at the temperature of thermoneutrality, plus the increment due to uncontrolled activity during the measurement period. Since the error due to activity is probably very small, the relationship (2) should suffice for fairly accurate estimates of the basal energy cost of the meadow vole. Varying environmental temperatures in the field change this energy cost. The correction factor for different temperatures was not assessed during this study. Morrison and Ryser (1951) reported that the oxygen consumption of *Microtus pennsylvanicus* increased 0.139 cc/gm hr for every 1°C decrease in temperature.

Maintenance energy consumption

A second objective of this study was to provide an estimate of energy consumption of the animal which would be referable to 'natural conditions.' The regression line of Fig. 4 has a b value which is not significantly different from that of the regression line of Fig. 3. Obviously the underlying relationship between oxygen consumption and body weight ("metabolic body size" of Brody 1945) is not changed by providing the voles with food and water and permitting at least a minimum amount of activity. The 95% confidence limits of the regression line:

(3) $Y = 20.6\,X^{.52}$ (Fig. 4)

are 0.39 and 0.65. The upper confidence limit, if rounded off to the nearest decimal, would be identical with the rounded off figure for b given by Brody (1945), 0.7. It seems quite reasonable to suppose that the underlying relationship between metabolism and body weight is valid regardless of species but that different species, even within a single order or family, may often show fairly large differences in the slope of the regression line relating metabolism to body weight.

Applying the caloric equivalent of oxygen to equation (3) we have:

(4) $\text{gcal/vole day} = 20.6(\text{body weight in gms.})^{.52} \times 4.825 \times 24 = 2386(\text{body weight in gms.})^{.52}$

In contrast to the previous estimate of energy consumption derived from fasting metabolic data, equation (4) estimates the total maintenance energy cost to the animal. The voles generally exhibited a slight increase in weight during a 24-hour period of measurement but this productive energy use is not indicated by the oxygen consumption. If equation (4) is applied to a field situation, the level of activity in the metabolism chamber must be assumed equal to the activity exhibited in the field. Since voles are undoubtedly more active under natural conditions, energy values so obtained must be regarded as minimum estimates.

The range of hourly rates of oxygen consumption was calculated for each weight class and plotted in Fig. 5. The amplitude becomes progressively greater as the weight of the animal decreases. The maximum rate of oxygen consumption tends to follow the same logarithmic curve as the average hourly rate. The minimum rate shows a more nearly linear relationship to weight. The anomalous result in the 30 to 35 gram weight class is assumed to be due to the small number of animals that were averaged. In animals of similar body conformation the energy cost of a stated increment of work, or activity, should be proportional to body weight to the power 1.0 whereas the basal metabolic rate should show a logarithmic relationship to body weight (Brody 1945). In Fig. 5, the difference between average mean hourly rate and average maximum rate is much greater for young animals than for adults, showing that the younger animals exhibited activity periods which were more intense and/or of longer duration than those of the older, heavier animals. Even more interesting, the minimum rate of oxygen consumption does not show a logarithmic relationship to body weight, indicating that the younger animals are capable of more complete relaxation, at least under the conditions of the experiment. This phenomenon is readily seen in many of the larger mammals, including man.

Activity patterns

The small absolute difference in the amounts of oxygen consumed during the night over that consumed during the day for the wild trapped voles actually represents a greater night/day difference in amount of activity than is at first apparent. This is because a continuous basal level of oxygen consumption is maintained even in the absence of activity, thus making a rather large absolute increase in activity appear only as a small percentage increase in total oxygen consumption.

The 2 to 3 hour "short cycle" of activity is in close agreement with the work of other investigators already cited. However, merely showing the existence of such cyclic phenomena does not necessarily shed any light on their origin. Most workers explain the "short cycle" as a product of feeding activity. It has not always been made clear whether this term refers to the muscular activity connected with food gathering, to the increased alertness of the animal during feeding, or to some more subtle energy cost such as specific dynamic action. Any of these fit the definition of activity in a physiological sense. Mann (pers. comm.) believes that feeding may be only vaguely connected with the "short cycle" of activity.

Voles whose oxygen consumption was measured the day following capture possessed a well defined 24-hour cycle, while voles retained in captivity for periods of from 3 to 8 days lacked such a cycle. After the initial loss of the 24-hour cycle, diel variation in the oxygen consumption showed only random changes. Captivity did not affect the overall tendency for voles to be more active at night than in the day, nor did the "short cycle" of activity disappear.

The activity pattern of *Microtus pennsylvanicus* is quite labile in comparison to that exhibited by genera such as *Peromyscus* or *Mus*. The conflicting literature suggests that the activity pattern may vary seasonally, geographically, or both.

The 24-hour cycle must be conditioned by factors other than, or in addition to, photoperiod since diel variation in activity was not maintained under captivity, where photoperiod duration was the same as in the field. Two major environmental factors which differed from field conditions were light intensity and temperature. Calhoun (1945-46) states that most animals which are subject to fluctuations of light in their normal habitat possess a 24-hour cycle of activity and that this cycle is inhibited by continuous light. However, in an earlier paper Calhoun (1945) mentions temperature as having an important effect on cycles. I. measured temperatures prevailing in *Microtus* runways during the summer of 1957 and found that they often exceed 40°C during the middle of the day. Animals which were active during these times would be exposed to temperatures well above the lethal limit. If temperature is not the primary conditioner for cyclic activity in *Microtus pennsylvanicus* it would certainly have a great modifying effect on any activity pattern induced by other environmental factors.

SUMMARY

1. The temperature range of thermoneutrality in *Microtus pennsylvanicus* lies between 25 and 29°C.
2. Huddling by voles, even within the temperature range of thermoneutrality, lowers the oxygen consumption.
3. The rate of oxygen consumption has a definite relationship to weight. For fasting animals this relationship is expressed by equation:

(1) Oxygen consumption as cc/vole hour $=$ $9.2(\text{body weight in gms})^{.64}$

For non-fasting, active animals the relationship is shown by equation:

(2) Oxygen consumption as cc/vole hour $=$ $20.6(\text{body weight in gms})^{.52}$

There was no significant difference between the slopes of the 2 equations.
4. Using the caloric equivalent of oxygen, equations (1) and (2) provided a means of estimating the minimum energy cost (equation 1) and total

energy utilization, exclusive of productive processes (equation 2), of a vole of known weight.

5. Young animals were capable of more intense bursts of activity and of more complete relaxation.
6. The meadow voles used in this study exhibited a "short cycle" of oxygen consumption whose mean duration was 3.6 hours.
7. In every case but one, the mean rate of oxygen consumption was highest during the night.
8. Newly captured voles possessed a bimodal diel activity pattern. Animals held in captivity did not show this pattern.
9. Temperature probably is very important in conditioning the 24-hour activity pattern of *Microtus pennsylvanicus* under field conditions.

REFERENCES

Brody, S. 1945. Bioenergetics and growth. New York, Reinhold.

Calhoun, J. B. 1945. Diel activity rhythms of the rodents *Microtus ochrogaster* and *Sigmodon hispidus hispidus* Ecology **26**: 251-273.

———. 1945-46. Twenty-four hour periodicities in the animal kingdom. II— the vertebrates. Jour. Tenn. Acad. Sci. **20**: 228-232; 291-308; 373-378; **21**: 208-216; 281-282.

Chambers, W. H. and W. H. Summerson. 1950. Energy metabolism. Annual Rev. Physiol. **12**: 289-310.

Davis, D. H. S. 1933. Rhythmic activity in the short-tailed vole (*Microtus*). Jour. Animal Ecol. **2**: 232-238.

Dice, L. R. 1922. Some factors affecting the distribution of the prairie vole, forest deer mouse, and prairie deer mouse. Ecology **3**: 29-47.

Emlen, J. T., R. L. Hine, William A. Fuller, and P. Alfonso. 1957. Dropping boards for population studies of small mammals. Jour. Wildlife Mgt. **21**: 300-314.

Fuhrman, G. J., E. D. McLin, and M. L. Turner. 1946. The effect of time of day on the metabolic rate of albino mice. A manometric method. Amer. Jour. Physiol. **147**: 284-288.

Hamilton, W. J. 1937a. Growth and life span of the field mouse, Amer. Naturalist **71**: 500-507.

———. 1937b. Activity and home range of the field mouse, *Microtus pennsylvanicus* (Ord.) Ecology **18**: 255-263.

Hart, J. S. 1950. Interrelations of daily metabolic cycle, activity, and environmental temperatures of mice. Canad. Jour. Research, D. **28**: 293-307.

———. 1952. Use of daily metabolic periodicities as a measure of the energy expended by voluntary activity of mice. Canad. Jour. Zool. **30**: 83-90.

Hatfield, D. M. 1939. Rate of metabolism in *Microtus* and *Peromyscus*. Murrelet **20**: 54-56.

———. 1940. Activity and food consumption in *Microtus* and *Peromyscus*. Jour. Mammal. **21**: 29-36.

Hatt, R. 1930. The biology of the voles of New York. Roosevelt Wildlife Bull. **5**: 513-623.

Kleiber, M. 1947. Body size and metabolic rate. Physiol. Rev. **27**: 511-541.

Maclagan, N. F. and M. M. Sheahan. 1950. The measurement of oxygen consumption in small animals by a closed circuit method. Jour. Endocrinology **6**: 456-462.

Mann, P. M. 1954. Diel activity rhythms of several species of small mammals. M.Sc. Thesis, U. of Western Ontario, London. Ontario, Canada.

Morrison, P. R. 1948. Oxygen consumption in several small wild mammals. Jour. Cell. and Compar. Physiol. **31**: 69-96.

——— **and F. Ryser.** 1951. Temperature and metabolism in some Wisconsin mammals; *Mus, Peromyscus, Clethrionomys, Zapus, Eutamias, Microtus, Mustella, Glaucomys, Scalopus, Rattus, Citellus, Blarina.* Federation Proc. **10**: 93-94.

Pearson, O. P. 1947. The rate of metabolism of some small mammals. Ecology **28**: 127-145.

Sealander, J. A. 1952. The relationship of nest protection and huddling to survival of *Peromyscus* at low temperatures. Ecology **33**: 63-71.

Seton, E. T. 1909. Life histories of northern animals. New York, Charles Scribners Sons.

Siegel, S. 1956. Non-parametric statistics for the behavioral sciences. New York, McGraw-Hill Co.

Snececor, G. W. 1956. Statistical methods. Ames, Iowa State Coll.

Welsh, J. H. 1938. Diurnal rhythms. Quart. Rev. Biol. **13**: 123-139.

THE RELATION OF ENERGY REQUIREMENTS OF TROPICAL FINCHES TO DISTRIBUTION AND MIGRATION

GEORGE W. COX
Department of Zoology, University of Illinois[1]

INTRODUCTION

The necessity for maintenance of a favorable energy balance is one of the major ultimate factors controlling bird distribution. Many of the various morphological, physiological and behavioral adaptations to a particular niche enable the bird to obtain adequate amounts of energy and specific nutrients for maintenance and reproduction. Migration, for example, shifts the bird to an environment where it can maintain a favorable balance during a period which would be critical without migration.

Environmental factors such as temperature and photoperiod exert a direct effect on energy balance, and the extent of the intrinsic ability of the bird to adjust to these factors sets physiological limits to distribution. Although in many cases the exact limits of distribution are determined by such factors as food niche competition or lack of suitable breeding habitat, it is important to analyze the effects of temperature and photoperiod to determine the overall limits which they impose.

---

[1] Present address: Biology Department, University of Alaska, College, Alaska.

Previous studies on the permanent resident house sparrow, *Passer domesticus,* indicate that this species maintains a favorable energy balance throughout the year by adjusting physiologically to yearly changes in temperature and photoperiod (Kendeigh 1949, Siebert 1949, Davis 1955). In the migratory white-throated sparrow, *Zonotrichia albicollis,* and slate-colored junco, *Junco hyemalis,* Siebert (1949) found that migration was necessary for maintenance of a favorable energy balance in winter. West (1958) also showed this to be true for the tree sparrow, *Spizella arborea,* but found that the energy balance was more favorable in the winter range (Illinois) during the summer than in the actual summer range (northern Manitoba). Thus the spring migration of this species is controlled by factors other than the effects of temperature and photoperiod on the energy balance.

The present study was designed to investigate the energy balance of resident tropical species of birds in order to understand how they are adjusted to live under nearly uniform photoperiods and constant high temperatures, and why migration does not occur.

The writer wishes to express his sincere appreciation to Dr. S. C. Kendeigh for suggesting the problem and for giving valuable advice and assistance through the course of the work. Thanks are especially due Dr. M. Moynihan, Resident Naturalist at the Canal Zone Biological Area, and his staff for making facilities at the laboratory available and for assistance in the installation and maintenance of experimental equipment. Appreciation is extended to my wife, Carolyn Cox, for help with much of the experimental work, and to Sr. Ivan Lloyd for furnishing hygrothermograph data during the period of work. This project was financed by grant G6425 from the National Science Foundation.

Experiments at Constant Temperatures

In order to determine the effect of temperature and photoperiod on energy requirements, metabolism was measured at 12- and 15-hour photoperiods and at a series of temperatures ranging from +4.4°C to +38.9°C. These experiments were done at the Canal Zone Biological Area, located on Barro Colorado Island, Panama Canal Zone, from February 8 to September 15, 1959.

Procedure

The principal species used in the experimental work was the variable seedeater, *Sporophila aurita,* with supplementary data being obtained from the yellow-bellied seedeater, *Sporophila nigricollis,* the blue-black grassquit, *Volatinia jacarina,* and the green-backed sparrow, *Arremonops conirostris.* Birds were trapped with mist nets in forest edge and open field areas on the mainland close to the laboratory and, when possible, weighed immediately following capture. Sexes could be determined externally in adults of all species except the green-backed sparrow where sexes were determined by dissection at the end of the experiments.

Following capture, birds were confined in temporary holding cages, measuring .76 meters on a side, until they became adjusted to captivity. During this period they were introduced gradually to the experimental food by mixing it in increasing quantities with commercial bird seed, which approximated their natural diet more closely. Mortality was 20-25% for the seedeaters and grassquit and none for the green-backed sparrow during this period.

Metabolism was measured by a procedure based on food consumption, which was introduced by Kendeigh (1949). The same method has been used subsequently by Siebert (1949), Davis (1955), and West (1958). The total caloric value of the excrement produced (excretory energy) is subtracted from that of the food ingested (gross energy intake) to give the energy metabolized or stored (metabolized energy). When constant weight is maintained, metabolized energy is regarded as existence energy, that is, the energy necessary for minimal activity and basic physiological processes. Maximum productive energy is calculated as the difference between existence energy at a given temperature and the maximum value of metabolized energy (potential energy), which apparently occurs at the lowest tolerated temperature. Productive energy represents energy available for activities other than existence.

For experimental work, birds were placed in individual cages measuring 15 × 30 × 30 cm. These were constructed of metal sheeting (lower half) and 1.3 cm mesh hardware cloth (upper half). Three to 6 days were allowed for the birds to become adjusted to the cages.

Metabolism was measured over 3-day periods. At the beginning and end of each run the birds were weighed, the amount of externally visible fat evaluated, and the amount of molt recorded. Birds were weighed on a triple-beam balance accurate to 0.01 g. Fat was recorded in terms of 6 classes (class 0—no fat; class 5—very heavy fat). Molt was evaluated on a similar scale, based on feathers found in the cage and sheathed feathers on the body, but only a negligible amount was noted during the experiments.

The food used was University of Illinois baby chick mash number 521, which was ground fine enough to pass through 1/16 inch mesh screening. Measured amounts, varying from 25 to 100 g depending on the experimental temperature, were placed in the cages at the beginning of each run. Water was available *ad libitum*.

At the end of each run the remaining food and excrement were collected from each cage and placed in a drying oven at 105°C for 3 or 4 days. Following this, separation was effected by rubbing the mixture gently over a sieve of 1/16 inch mesh screening. Dry weights of the feces and uneaten food were recorded and the feces preserved for calorimetric analysis.

Moisture content determinations were made for each batch of feed. These determinations varied from 10.4 to 12.0%. From these values, the dry weight of the food presented to the birds was calculated. The caloric value of the food was measured in a Parr adiabatic oxygen bomb calorimeter. Values ranged from 4.199 to 4.332 kcal/g dry weight (10 determinations for each batch). Values determined for each batch of food were used to calculate data for birds being fed the same batch.

Two thermostatically controlled walk-in cabinets, each measuring 1.9 meters on a side, provided the experimental temperatures. Fluctuations of temperature in these rooms were approximately ±1.1°C. Photoperiod was regulated by automatic time switches. Humidity was not controlled and varied widely. At low temperatures, relative humidity varied from 94-100% at 18°C to 85-100% near 0°C. At high temperatures, it varied from 46-57% at 35°C to 31-38% at 42°C. Under outdoor conditions during the dry season (daily mean temperature range of 26-30°C) mean humidity varied from 89 to 63% and during the rainy season (daily mean temperature range of 26-29°C) from 95 to 75%. Air movement was appreciable in both temperature rooms in order to prevent temperature stratification but was noticeably higher in the low temperature room. Light was furnished by three 100-watt bulbs in the low temperature room and two 150-watt bulbs in the high temperature room.

Statistical procedures were taken from Ostle (1954) and Dixon and Massey (1957). A probability level of 0.01 was required for comparisons to be considered significant unless otherwise indicated.

Weights and fat classes

The only species with a marked sex difference in weight is the green-backed sparrow in which males average significantly heavier than females (Table I). Female variable seedeaters tend to be heavier than males (significant at 0.05 level). Fat classes in freshly caught birds averaged less than 1.0 in all species.

TABLE I. Weights and fat classes of freshly captured birds

Sex	Number captured	Average weight ± S. E.	P
		Variable seedeater	
M	15	10.53± .17	
F	25	10.96± .12	0.05
M+F	40	10.80+ .10	
		Green-backed sparrow	
M	7	40.84±1.03	
F	5	36.71±1.17	0.01
M+F	12	39.12± .94	
		Blue-black grassquit	
M	2	9.12± .49	
F	2	9.49± .50	0.30
M+F	4	9.30± .23	
		Yellow-bellied seedeater	
M	3	9.24± .18	
F	5	8.70± .15	0.10
M+F	8	8.90± .14	

Birds lost weight following capture and introduction into experimental cages but, after a brief period of adjustment, regained normal weight which they then maintained. Weights of experimental birds maintained under outdoor conditions or at constant normal temperatures at 12- and 15-hour photoperiods were not significantly different from weights of freshly caught birds.

Under experimental conditions there were no significant differences between weights of male and female variable seedeaters. Male green-backed sparrows, however, averaged 2-7 g heavier than females (Table II). In 10 birds under outdoor conditions this difference was significant at the 0.025 level. Sex differences were not tested in other species because of the small numbers used. Blue-black grassquits and yellow-bellied seedeaters, however, showed no constant relationship between sex and weight.

No significant difference in weight between corresponding temperatures at the 2 photoperiods were found in the variable seedeater (Table II, III). Weight tended, however, to decrease at higher temperatures, especially above 28-29°C. In the variable seedeater the drop in weight between 28.4°C and 38.9°C at 15 hours was significant (0.01 level). Weights at 10°C for both pho-

TABLE II. Weights (grams) and fat classes of green-backed sparrows under experimental conditions

Temp. (°C)	Males			Females		
	No.	Av. weight ± S.E.	Av. fat class	No.	Av. weight ± S.E.	Av. fat class
Outdoors						
Dry season (28.2).........	6	41.91±0.93	1.5	4	37.92+1.08	1.0
12-hour photoperiod						
10.0...........	2	45.24±0.69	1.9	2	38.01±0.55	1.5
18.3...........	3	42.20±1.97	1.2	2	36.64±1.72	1.2
28.8...........	3	40.20±0.31	1.6	2	37.80±0.62	1.2
35.0...........	3	34.69±0.39	0.2	2	32.06±0.46	0.1
38.9...........	2	32.00±1.02	0.2	2	27.28±0.80	0.0
15-hour photoperiod						
4.4...........	—	—	—	2	35.10±0.02	1.3
10.0...........	—	—	—	2	35.68±0.38	1.4
18.3...........	2	39.20±3.16	2.0	2	35.74±0.88	1.9
28.4...........	3	37.02±0.24	0.6	2	33.77±0.63	0.6
35.0...........	2	37.78±0.08	1.0	3	33.93±1.02	0.8

toperiods were significantly higher (0.025 and 0.05 levels) than those at 28-29°C. At the 15-hour photoperiod and at a temperature of 4.4°C, which approaches the lethal limits of 0°C, variable seed-eaters showed a sharp decrease in weight from that at 10°C (significant at 0.05 level).

Average fat classes at lower temperatures showed little relation to weight, although at least part of the increased weight was probably due to fat deposition. At high temperatures average fat classes decreased sharply in most cases.

In all but one case (outdoors, wet season), metabolism per bird day tended to be slightly higher in heavier individuals of the variable seedeater. These differences were not statistically significant, however, except at extreme high and low temperatures where average fat classes were low and weight differences therefore more closely represented differences in lean weight. Comparisons on the basis of gram bodyweight showed no significant differences in any instance.

Gross energy intake

Measurements of gross energy intake, excretory energy, and metabolized energy at different temperatures and photoperiods were tested with an analysis of variance technique appropriate to a complete block design with a factorial arrangement of treatments (Ostle 1954, pp. 342-350). Specifically the design was a 2 (photoperiods) × 4 (corresponding temperatures at the photoperiods) factorial, with individual birds being treated as replicates. Although the same individuals were frequently used at different temperatures, for purposes of analysis it was assumed that previous treatment did not influence the response at a given temperature. This analysis tested differences attributable to temperature, photoperiod (the level of metabolism at the 2 photoperiods) and the interaction of photoperiod and temperature (the rate of change of metabolism with change of temperature at the 2 photoperiods).

Probability values from these tests are given in the tables showing linear regression formulas. Since calculations of the regression lines in some cases included data from temperatures with no counterpart at the alternate photoperiod, this test does not actually apply to the regression lines themselves. Data for the green-backed sparrow and yellow-bellied seedeater were too incomplete to be tested by the above method. In addition, results for the yellow-bellied seedeater at 15 hours are based mostly on a single bird and are therefore unreliable. These data have been omitted from

TABLE III. Weights (grams) and fat classes of variable seedeaters, blue-black grassquits and yellow-bellied seed-eaters under experimental conditions

Temp. (°C)	Variable Seedeater			Blue-Black Grassquit			Yellow-Bellied Seedeater		
	No. birds	Av. Wt. ± S.E.	Av. fat class	No. birds	Av. Wt. ± S.E.	Av. fat class	No. birds	Av. Wt. ± S.E.	Av. fat class
Outdoors									
Dry season (28.2).	13	10.56±0.16	1.8	5	9.74±0.18	3.8	5	8.96±0.41	1.4
Wet season (26.9).	10	10.48±0.15	1.2	—	—	—	—	—	—
12-hour photoperiod									
10.0.............	14	11.21±0.15	2.5	5	9.56±0.17	3.3	5	9.96±0.27	2.1
18.3.............	15	10.52±0.14	2.8	5	9.46±0.24	4.4	5	10.15±0.25	3.8
28.8.............	15	10.70±0.18	2.8	5	9.56±0.22	4.2	5	8.92±0.27	1.3
35.0.............	15	10.34±0.16	1.7	5	9.18±0.35	3.7	5	8.92±0.29	2.3
38.9.............	—	—	—	5	9.29±0.12	3.1	5	8.84±0.39	2.3
15-hour photoperiod									
4.4.............	14	10.61±0.14	1.4	4	9.49±0.15	2.4	1	9.57	1.3
10.0.............	15	10.97±0.13	2.4	5	9.93±0.37	3.5	1	10.11	2.2
18.3.............	15	10.86±0.18	3.1	5	10.02±0.42	3.9	1	9.70	2.8
28.4.............	15	10.58±0.15	3.4	5	9.83±0.21	4.9	5	8.72±0.20	1.7
35.0.............	15	10.67±0.17	2.8	5	9.16±0.21	2.7	—	—	—
38.9.............	15	9.64±0.13	1.3	5	9.50±0.12	2.8	—	—	—

discussions. Separate regression lines were not calculated for male and female green-backed sparrows despite the marked difference in weight because of the small number of birds used.

It has been shown repeatedly that food intake increases linearly with decreasing temperature below the zone of thermoneutrality (Kendeigh 1949, Davis 1955, West 1958). This was true of all species in the present study (Table IV). Linear regression formulas for gross energy intake per bird day were similar for the 3 smallest species. In the heavier green-backed sparrow the level of intake was higher and the rate of increase with decreasing temperatures was greater. Differences in gross energy intake per bird between the 2 photoperiods were not significant in the variable seedeater, but in the blue-black grassquit the level of intake was significantly greater (0.05 level) at the longer photoperiod. There were no significant differences between photoperiods in the rate of increase with drop in temperature.

TABLE IV. Linear regression formulas for gross energy intake in relation to temperature (°C) and photoperiod

Species	Photoperiod (hrs)	Regression formula (kcal)	P Photoperiod	P Temp. × Photo.
		Gross energy/bird day		
Variable seedeater...	12	21.132 — 0.382T	0.05	0.05
	15	23.219 — 0.446T		
Blue-black grassquit.	12	18.083 — 0.346T	0.05	0.05
	15	20.381 — 0.403T		
Green-backed sparrow	12	42.462 — 0.797T	—	—
	15	44.152 — 0.804T		
Yellow-bellied....... seedeater	12	18.885 — 0.345T	—	—
	15	23.895 — 0.520T		
		Gross energy/bird hour of light		
Variable seedeater...	12	1.710 — 0.030T	0.01	0.05
	15	1.548 — 0.030T		
Blue-black grassquit.	12	1.495 — 0.028T	0.01	0.05
	15	1.361 — 0.027T		
Green-backed sparrow	12	3.536 — 0.066T	—	—
	15	2.949 — 0.054T		
Yellow-bellied....... seedeater........	12	1.580 — 0.029T	—	—
	15	1.607 — 0.036T		

The hourly rate of food intake was significantly higher at the shorter photoperiod (Table IV). The rate of increase of food intake per hour with decreasing temperatures was significantly greater at the 15-hour photoperiod in both the variable seedeater and blue-black grassquit (0.05 level).

Excretory energy

In the house sparrow, Kendeigh (1949) found that the caloric value of the excrement increased with decreasing temperatures, while Siebert (1949) noted the lowest value at 22°C. Davis (1955) and West (1958), however, found no significant variation in per gram fecal energy with temperature. In the present study, involving 89 determinations for the variable seedeater, 18 each for the green-backed sparrow and yellow-bellied seedeater, and 21 for the blue-black grassquit, no significant variation with temperature was found. Averages of all determinations by species were (kcal/g ± S. E.) 3.479 ± .014 for the variable seedeater, 3.549 ± .024 for the yellow-bellied seedeater, 3.400 ± .013 for the green-backed sparrow, and 3.481 ± .023 for the blue-black grassquit. The value for the green-backed sparrow was significantly lower than those for other species (0.025 level with the variable seedeater, 0.01 level with other species). The value for the yellow-bellied seedeater was significantly greater than that of the variable seedeater (0.05 level). Other comparisons were not significant.

Regression formulas for excretory energy are summarized in Table V. There were no significant differences in the level of excretory energy per bird day at the 2 photoperiods. The rate of change with temperature was significantly less (0.05 level) at the 15-hour photoperiod in both the variable seedeater and blue-black grassquit.

Excretory energy loss per hour of daylength was significantly higher at the shorter photoperiod. The rate of increase of excretory energy per hour

TABLE V. Linear regression formulas for excretory energy in relation to temperature (°C) and photoperiod

Species	Photoperiod (hrs)	Regression formula (kcal)	P Photoperiod	P Temp. × Photo.
		Excretory energy/bird day		
Variable seedeater...	12	5.134 — 0.100T	0.05	0.01
	15	4.877 — 0.091T		
Blue-black grassquit.	12	4.124 — 0.080T	0.05	0.05
	15	3.887 — 0.073T		
Green-backed sparrow	12	13.081 — 0.244T	—	—
	15	13.682 — 0.250T		
Yellow-bellied....... seedeater	12	4.698 — 0.083T	—	—
	15	6.074 — 0.135T		
		Excretory energy/bird hour daylength		
Variable seedeater...	12	0.418 — 0.008T	0.01	0.01
	15	0.324 — 0.006T		
Blue-black grassquit.	12	0.351 — 0.007T	0.01	0.01
	15	0.263 — 0.005T		
Green-backed sparrow	12	1.099 — 0.021T	—	—
	15	0.918 — 0.017T		
Yellow-bellied....... seedeater	12	0.391 — 0.007T	—	—
	15	0.406 — 0.009T		

with decreasing temperatures was significantly greater (0.01 level) at the longer photoperiod in the variable seedeater and blue-black grassquit.

Efficiency of food utilization

Efficiency of food utilization, measured as the ratio of food metabolized to the gross energy intake, has been shown to increase from low to high temperatures (Kendeigh 1949, Siebert 1949, West 1958). Davis (1955) found, however, that the highest efficiency occurred at 18°C in summer acclimated birds and suggested that this was due to the fact that this temperature approximated that to which they were naturally adapted.

Variation in efficiency values in the present study was small (Table VI). In the variable seedeater, efficiency values at the 12-hour photoperiod decreased regularly from 35°C to 10°C. However, at 15 hours, as temperatures decreased over the same range, efficiency remained high, decreasing only when the temperature reached 4.4°C. At 10°C efficiency values were higher for all species at the longer photoperiod. These data suggest that at the longer photoperiod a relatively high efficiency can be maintained through lower temperatures. This difference would seem to be related to the significantly lower hourly rate of feeding at longer photoperiods which would allow more time for digestion.

TABLE VI. Food utilization coefficients at different temperatures and photoperiods

Temp. (°C)	Variable seedeater	Green-backed sparrow	Blue-black grassquit	Yellow-bellied seedeater
Outdoors				
Dry S. (28.2)....	.75	.67	.79	.73
Wet S. (26.9)....	.81	—	—	—
12-hour photoperiod				
38.9............	—	.72	.78	.77
35.0............	.79	.68	.81	.73
28.8	.78	.69	.77	.75
18.3............	.77	.71	.81	.75
10.0............	.76	.68	.76	.75
15-hour photoperiod				
38.9............	.83	—	.83	—
35.0............	.78	.70	.78	—
28.4............	.79	.71	.79	.71
18.3............	.80	.67	.82	.73
10.0............	.80	.69	.81	.78
4.4............	.76	.70	.79	.73

Metabolized energy

Previous workers (Davis 1955, West 1958) have shown a tendency for house sparrows and tree sparrows to metabolize more at 15- than at 10-hour photoperiods, but have been able to show few statistically significant differences. Siebert (1949) found that metabolized energy in winter adapted house sparrows was significantly greater at high temperatures at a 15-hour photoperiod than at a 10-hour photoperiod. At low temperatures he found no significant differences.

In the present study, significant effects of photoperiod on metabolized energy per bird day were found (Table VII). In the variable seedeater and blue-black grassquit, values were higher (0.01 level) at the longer photoperiod, and the rate of increase with decrease in temperature was greater (0.05 level). In the green-backed sparrow and yellow-bellied seedeater levels of metabolized energy per bird per day were also higher at 15 hours.

TABLE VII. Linear regression formulas for metabolized energy in relation to temperature and photoperiod

Species	Photoperiod (hrs)	Regression formula (kcal)	P Photoperiod	P Temp. × Photo.
		Metabolized energy/bird day		
Variable seedeater...	12	15.988 — 0.282T	0.01	0.05
	15	17.999 — 0.340T		
Blue-black grassquit.	12	13.883 — 0.259T	0.01	0.05
	15	16.319 — 0.324T		
Green-backed sparrow	12	29.394 — 0.554T	—	—
	15	30.454 — 0.555T		
Yellow-bellied....... seedeater	12	14.209 — 0.262T	—	—
	15	17.966 — 0.401T		
		Metabolized energy/bird hour daylength		
Variable seedeater...	12	1.343 — 0.024T	0.01	0.05
	15	1.189 — 0.022T		
Blue-black grassquit.	12	1.166 — 0.022T	0.01	0.05
	15	1.095 — 0.022T		
Green-backed sparrow	12	2.446 — 0.046T	—	—
	15	2.032 — 0.037T		
Yellow-bellied....... seedeater	12	1.192 — 0.027T	—	—
	15	1.201 — 0.027T		
		Metabolized energy/gram day		
Variable seedeater...	12	1.438 — 0.024T	0.05	0.01
	15	1.703 — 0.033T		
Blue-black grassquit.	12	1.457 — 0.027T	0.05	0.05
	15	1.709 — 0.034T		
Green-backed sparrow	12	0.702 — 0.012T	—	—
	15	0.862 — 0.016T		
Yellow-bellied....... seedeater	12	1.385 — 0.023T	—	—
	15	1.813 — 0.038T		

Metabolized energy per hour of photoperiod was significantly lower at the longer photoperiod. The values for the yellow-bellied seedeater appear to be reversed, but are unreliable since most of the 15-hour data are from a single bird.

Metabolized energy per gram bodyweight also showed differences related to photoperiod. The rate of increase with decreasing temperatures in the variable seedeater was significantly greater at the longer photoperiod (0.01 level). In the blue-black grassquit, both the level of metabolized energy and the rate of change with temperature were higher (0.05 level) at the longer photoperiod. Values for the green-backed sparrow and yellow-bellied seedeater showed the same trend.

Tolerance of low temperatures

Low lethal temperatures were determined at 12- and 15-hour photoperiods for all species. From 10°C at 12 hours and 4.4°C at 15 hours, temperatures were gradually lowered (1°C every 3 days) until 50% mortality occurred. Since the low temperature walk-in room functioned to only 0°C, birds which survived to this point were transferred to a deep-freeze unit. This was an unsatisfactory arrangement since the highest temperature that could be maintained here was —4.0°C.

At 12 hours, the lowest temperature tolerated by the variable seedeater (14 birds), yellow-bellied seedeater (5 birds), and blue-black grassquit (5 birds) was +2.8°C. At the 15-hour photoperiod these species survived to 0°C (variable seedeater, 14 birds; blue-black grassquit, 5 birds; yellow-bellied seedeater, 1 bird). At both photoperiods the green-backed sparrow (5 birds at 12 hours, 2 birds at 15 hours) survived temperatures of —7.4°C but died when shifted to —9.4°C (numbers of birds are total used).

The lower limits of tolerance do not seem to be related to the hourly rate of feeding itself since birds at 15 hours which had lower hourly feeding rates, survived to lower temperatures. The limits are probably related to the maximum ability of the bird to metabolize food per day.

The ability to survive to lower temperatures at the 15-hour photoperiod may in part be due to the fact that at this day-length less energy must be stored to last the bird overnight. Also the increased number of hours for feeding allowed a greater intake per day even though the hourly rate of feeding was less (Table VIII). A reduction in the feeding rate equivalent to the increase in length of the feeding period (3 hours) so that the total daily intake remained the same would result in metabolized energy per hour at 15 hours being 80% of that at 12 hours. In the variable seedeater at temperatures from 35°C to 18.3°C the hourly rate of feeding at 15 hours was reduced almost proportionately (to 82-86% of that at 12 hours), but at 10°C the hourly rate increased to 90% of the rate at 12 hours.

Tolerance of high temperatures

To determine high lethal temperatures, the temperature was raised gradually (1°C per 3 days), starting with 35°C. At 12 hours the variable seedeater (15 birds) and green-backed sparrow (4 birds) survived to 38.9°C, the yellow-bellied seedeater (5 birds) to 40.6°C, and the blue-black grassquit (5 birds) to 42.2°C. At 15 hours the variable seedeater (15 birds) and green-backed sparrow (5 birds) survived to 41.7°C, and the blue-black grassquit (5 birds) to 43.9°C (numbers are total birds used). These limits of tolerance correlate roughly with the niches of the species in the wild. The green-backed sparrow is characteristically a forest-edge species, foraging less in open areas than the others. The variable seedeater feeds largely on grasses in open areas, but retires to thickets during most of the middle of the day. The yellow-bellied seedeater and blue-black grassquit are the most typical species of open areas, although even they retire to sheltered places during the hottest part of the day.

TABLE VIII. Relative rates of metabolized energy intake at 12- and 15-hour photoperiods

Temp. (°C)	PERCENT THAT METABOLIZED ENERGY PER HOUR AT 15 HOURS IS OF THAT AT 12 HOURS		
	Variable seedeater	Blue-black grassquit	Green-backed sparrow
35.0	84	102	101
28.8	86	78	80
18.3	82	83	82
10.0	90	94	80

The limits of tolerance of these species seemed to be related to the length of the dark period when the birds could not obtain water, since mortality was usually noted in the early morning and the dead birds were extremely desiccated.

Metabolized energy values at 38.9°C were higher than expected from regression lines calculated through data from lower temperatures. Values of metabolized energy per bird day for all species at 35.0°C and 38.9°C were not significantly different, although in all but one case they were lower at the higher temperature (Table IX). The fact that most values were lower at the higher temperature is in part due to the fact that birds were lighter at this temperature. When compared on the basis of per gram bodyweight, metabolized energy values at the 2 temperatures were even more similar.

EXPERIMENTS UNDER OUTDOOR CONDITIONS

Metabolism measurements were made under outdoor conditions during dry and rainy seasons to provide controls for the experiments at constant temperatures. During the dry season metabolism was measured from March 12 to April 5 in all 4 species. Birds were placed in a vacant room in

TABLE IX. Metabolized energy at high temperatures

Species	Temp. (°C)	METABOLIZED ENERGY PER BIRD DAY (kcal)		METABOLIZED ENERGY PER GRAM WT. DAY (kcal)	
		12 hrs	15 hrs	12 hrs	15 hrs
Variable seedeater	35.0	6.291±0.184	6.508±0.152	0.609±0.015	0.603±0.010
	38.9	—	6.355±0.163	—	0.660±0.016
Green-backed sparrow	35.0	9.685±0.299	12.220±0.474	0.286±0.010	0.345±0.017
	38.9	8.750±0.284	—	0.300±0.008	—
Yellow-bellied seedeater	35.0	5.352±0.157	—	0.602±0.015	—
	38.9	5.001±0.309	—	0.571±0.045	—
Blue-black grassquit	35.0	4.654±0.058	5.903±0.257	0.504±0.033	0.647±0.030
	38.9	4.778±0.227	5.804±0.084	0.515±0.019	0.613±0.001

one of the laboratory buildings where windows on 2 sides allowed outdoor temperatures to be maintained. In this location there was no disturbance by human activity. During the rainy season, variable seedeaters were again run from August 22 to 31. Other species were not used because of difficulties in obtaining birds. The rainy season controls were placed in a shielded corner of a large screened aviary building where outdoor temperatures prevailed. In this location there was a slight amount of human interference. In both locations birds were exposed to natural fluctuations of photoperiod, temperature, and humidity, but were shielded from precipitation. Methods of handling birds were identical with those used under constant conditions.

There were slight differences in certain environmental conditions between the periods during which these 2 groups were run (Table X). During the rainy season temperatures averaged 1.3°C lower, relative humidity 11% higher, and photoperiod 10 minutes longer than during the dry season.

TABLE X. Climatic conditions during dry and rainy season runs

	Dry season	Rainy season
Mean daily temp. (°C)	28.2	26.9
Max. temp. range (°C)	25.6-31.1	25.0- 29.4
Av. daily temp. range (°C)	3.5	2.9
Relative humidity (hourly av.)	81	92
Max. humidity range (percent)	53-93	71-100
Av. humidity range (percent)	64-89	79- 96
Av. photoperiod (hours	12.2	12.3

In the variable seedeater, values for metabolized energy per bird day (Table XI) were significantly lower (0.01 level) under dry season conditions than at the experimentally maintained 12-hour photoperiod and 28.8°C (7.656 ± .184 kcal). This difference was also significant when compared on the basis of gram body weight (.719 ± .021 kcal at 12 hours, 28.8°C). Other species showed no significant differences under these 2 conditions. This difference in the variable seedeater may represent an effect of fluctuating outdoor conditions. Metabolized energy in the variable seedeater under outdoor rainy season conditions was significantly higher in all comparisons with the 12 hour, 28.8°C data, and also significantly higher than values for the dry season controls. The birds used in these runs were freshly caught from populations in which most birds were in breeding condition. Although confined in small cages, males sang frequently, often in response to wild birds outside the aviary. Some extra activity may have been caused by human activity in the vicinity. This difference in metabolism seems to indicate that the birds were metabolizing at a higher than existence level, rather than being a response to the slight differences in climatic conditions between the dry and rainy seasons.

SEASONAL AND DISTRIBUTIONAL FACTORS AFFECTING ENERGY BALANCE

In order to understand how energy balance, as determined in the laboratory, may affect distribution in the wild, it is necessary to analyze the climatic conditions to which the birds are naturally exposed. Also, it is important to know how energy demanding activities such as reproduction and molt are distributed through the year.

At Barro Colorado Island (latitude 9°N) yearly variation in temperature and photoperiod is small (Figure 1). Mean monthly temperature varies only 1.5°C from January to April, and the maximum variation in photoperiod is one hour (11.6-12.6 hours). Marked dry and wet seasons occur during which rainfall varies from less than 2 inches in February to over 19 inches in November. During the dry season (Jan.-Apr.) temperatures are

TABLE XI. Metabolized energy of birds under dry season and rainy season outdoor conditions

Species	No. birds	Metabolized energy per bird day (kcal)	Metabolized energy per bird hour (kcal)	Metabolized energy per gram day (kcal)	Digestive Efficiency (percent)
Dry season					
Variable seedeater..........	13	6.841±0.143	.559±0.011	.648±0.010	75
Green-backed sparrow......	10	14.121±0.368	1.162±0.030	.353±0.013	67
Blue-black grassquit........	5	6.358±0.105	.521±0.010	.655±0.019	79
Yellow-bellied seedeater.....	5	5.830±0.544	.489±0.040	.648±0.035	73
Wet season					
Variable seedeater..........	10	10.324±0.197	.827±0.015	.992±0.024	81

slightly higher, humidity is lower, and percent sunshine is greater. Many species of trees lose the bulk of their leaves at this time, and the forest as a whole is about one-third defoliated. Tall grasses typical of open areas die, and at least in the vicinity of the Canal Zone, are burned off by man.

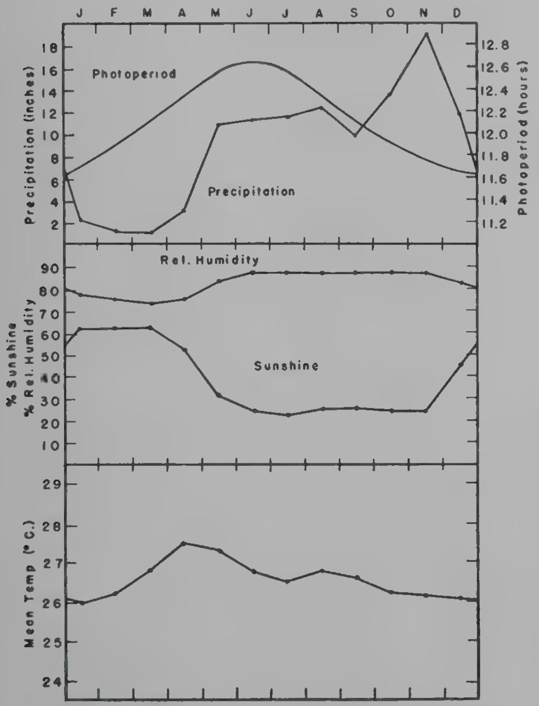

FIG. 1. Environmental conditions during the year in the vicinity of Barro Colorado Island. Data for relative humidity, percent sunshine and mean monthly temperatures are from Madden Dam, C. Z.

Even within the Canal Zone there is marked variation from place to place in the difference between dry and wet seasons. On the Caribbean coast the dry season is less severe, and the total yearly rainfall considerably higher than on the Pacific coast (130 in. at Cristobal, 70 in. at Balboa).

Since the species studied are permanent residents, the major energy demanding activities during the year are reproduction and molt.

In the Canal Zone, nesting by the variable seedeater, yellow-bellied seedeater, and blue-black grassquit begins one to 2 months after the beginning of the rainy season in late April. At this time vegetation in open areas has reached full development and grasses have begun to set seed. In the Canal Zone, nests with eggs of the variable seedeater have been recorded from the last week of May to September (Eisenmann 1952). In Costa Rica this species breeds mainly from late April, May, or June to September (early part of rainy season) with occasional nestings at the end of the rainy season in December and January (Skutch 1954). Skutch correlates time of nesting with the setting of seed by grasses. Nests with eggs of the yellow-bellied seedeater and blue-black grassquit have been recorded in the Canal Zone only in July (Eisenmann 1952).

The breeding season of the green-backed sparrow is slightly earlier. In the Canal Zone, nests with eggs have been found from late April through mid-July (Eisenmann 1952). Skutch states that in Costa Rica most nesting occurs from February to July with occasional nests as early as January or as late as August through October.

Adults of the seedeaters and grassquit feed mainly on seeds, particularly those of grasses. Thus these species nest during the period when food is most available and the least amount of energy need be expended in obtaining it. The green-backed sparrow is omnivorous, consuming a variety of fruits, seeds, and insects (Skutch). Since many species of trees flower during the dry season and produce fruit toward its end or during the early part of the wet season, the same situation is probably true in this species.

Definite data on time of molt was not obtained. However, birds of all species trapped between March 1 and the middle of August showed practically no evidence of molt. Only a negligible amount was recorded during the experiments. Therefore it seems likely that only a weak prenuptial molt, if any, occurs. The main molt would be the post-nuptial, probably taking place during the last half of the rainy season in all species.

From these rough data on reproduction and molt, it appears that these 2 energy demanding activities occur during the time of the year when the least amount of energy is required for obtaining food.

Although populations of these species from other locations, especially those of different subspecies, may react differently to temperature and photoperiod, it is of interest to note the extremes of these conditions to which each species is exposed (Table XII). Photoperiod data were obtained from Smithsonian Meteorological Tables (Smithsonian Institution 1951) and temperatures from World Weather Records, 1941-50 (U. S. Department of Commerce 1959).

Table XII. Ranges of temperature (°C) and photoperiod (hrs) at north and south latitudinal extremes of ranges

	Variable seedeater	Green-backed sparrow	Blue-black grassquit	Yellow-bellied seedeater
Southern limit				
Latitude	2° S	3° S	33° S	24° S
Longest day	12.2	12.3	14.3	13.6
Shortest day	12.0	11.9	10.0	10.6
Coldest month	23.8	18.6	14.2	14.3
Warmest month	25.7	26.4	27.2	21.6
Yearly mean	24.9	22.0	20.7	18.2
Northern limit				
Latitude	20° N	20° N	24° N	9° N
Longest day	13.3	13.3	13.6	12.6
Shortest day	10.9	10.9	10.6	11.6
Coldest month	25.6	23.1	19.9	18.8
Warmest month	29.9	28.0	28.3	21.1
Yearly mean	27.6	25.9	24.3	20.1

The range of the variable seedeater extends from Veracruz and Oaxaca, Mexico, south to southern Colombia (4 subspecies). The yellow-bellied seedeater ranges from southern Costa Rica through northeastern South America to Sao Paulo, Brazil (3 subspecies). The range of the blue-black grassquit is largest, extending from southern Sinaloa and Veracruz, Mexico, south through most of northern South America to northern Argentina in the province of Entre Rios (3 subspecies). The green-backed sparrow ranges from Chiapas and Campeche, Mexico, to the tropical areas of Ecuador, Colombia, and Venezuela (8 subspecies). Ranges are taken from Hellmayr (1938).

The northern limit of the variable seedeater and green-backed sparrow is about 20°N, at which latitude they are exposed to a photoperiod range of about 2.4 hours. Mean monthly temperatures vary somewhat more at these limits than at Barro Colorado Island (4.3°C for the variable seedeater, 4.9°C for the green-backed sparrow), but yearly means are very similar. The yellow-bellied seedeater reaches 24°S at Sao Paulo, Brazil, where the yearly photoperiod range is 3 hours. Temperatures at Sao Paulo average 8.4°C below those of the Canal Zone, and show a greater range (7.3°C). The blue-black grassquit reaches 33°S in Argentina where photoperiod variation is 4.3 hours. Mean monthly temperatures show a large range (13.0°C) but average only 5.9°C below those at Barro Colorado Island.

Discussion

It should be emphasized that although birds under experimental conditions could obtain food freely, and with a minimum expenditure of energy, food availability (as well as many other factors) in nature may have important effects on the energy balance.

Linear regression formulas were calculated for productive energy (Table XIII). Productive energy increased with increasing temperatures at a rate equal to the rate of decrease of metabolized energy. Productive energy was zero at the lowest temperature tolerated.

As West (1958) has pointed out, productive energy probably reaches a peak at a point some-

Table XIII. Linear regression formulas for productive energy in relation to temperature (°C) and photoperiod

Species	Photoperiod (hrs.)	Regression formula
		Productive energy/bird day
Variable seedeater	12 15	$0.282T-0.790$ $0.340T$
Blue-black grassquit	12 15	$0.259T-0.725$ $0.324T$
Yellow-bellied seedeater	12 15	$0.262T-0.734$ $0.401T$
Green-backed sparrow	12 15	$0.554T+11.080$ $0.555T+11.100$
		Productive energy/gram day
Variable seedeater	12 15	$0.024T-0.067$ $0.033T$
Blue-black grassquit	12 15	$0.027T-0.076$ $0.034T$
Yellow-bellied seedeater	12 15	$0.023T-0.064$ $0.038T$
Green-backed sparrow	12 15	$0.012T+0.240$ $0.016T+0.320$

what below the zone of thermoneutrality and then declines rapidly to zero at the upper lethal temperature. This is due to the fact that from the zone of thermoneutrality through higher temperatures, work tends to increase the body temperature toward the lethal level. Although no direct data were obtained on this point in the present study, it would appear that productive energy would reach a maximum in the vicinity of 30°C, since a leveling off of existence energy values, indicating no zone of thermoneutrality until temperatures of 35-38.9°C were reached.

The rate of increase of productive energy with temperature was greater at the 15-hour photoperiod than at the 12-hour photoperiod (Table XIII, Figure 2). Although the slope values of the regression lines for productive energy per bird day are almost identical for the 2 photoperiods in the green-backed sparrow, the slope value of metabolized energy per gram bodyweight was higher at the 15-hour photoperiod. This latter value is probably more significant in this species because of the marked difference in weight between the sexes. The high rate of increase of productive energy per bird in the green-backed sparrow is largely due to its great over-all size. Productive energy per gram bodyweight, however, showed a rate of increase with temperature much lower than that of other species.

Potential energy during the course of the year at Barro Colorado Island remains almost constant in all species since the yearly variation in photoperiod is small. The yearly cycle of existence and productive energy was determined by substituting monthly mean temperatures in the regression formulas for the 12-hour photoperiod. Since these temperatures show a range of only 1.5°C existence and productive energy likewise showed little variation.

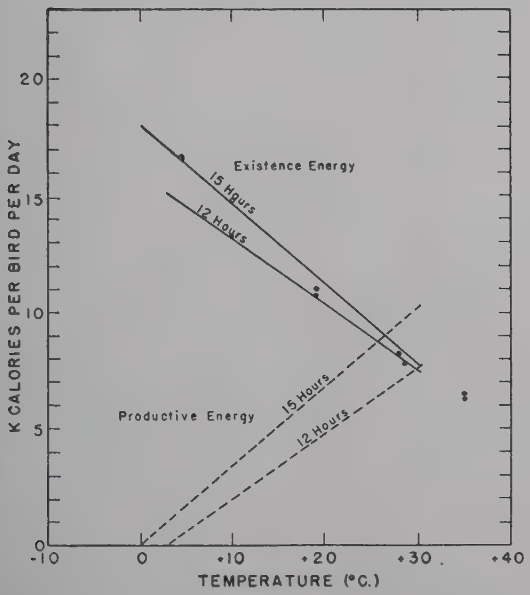

FIG. 2. Existence and productive energy for the variable seedeater at 12- and 15-hour photoperiods. Solid dots represent existence energy values at 12 hours; circles represent existence energy values at 15 hours.

Experiments at the 15-hour photoperiod have indicated in several ways that the energy balance is more favorable at this daylength than at 12 hours. Birds survived to lower temperatures at the longer daylength, showed a greater rate of increase of energy intake with decrease in temperature, maintained higher digestive efficiencies at lower temperatures, and had higher levels of productive energy. It should be noted that differences in metabolized energy between the 2 photoperiods are in large part due to the fact that the birds are active for 3 more hours per day at the longer photoperiod. This extended period of wakefulness results in higher body temperatures and a greater total amount of activity such as feeding movements. Thus the most significant advantages of the longer photoperiod seem to be the decreased length of the non-feeding period and the increased time for accumulating reserves for the non-feeding period.

Because of the favorable effects of the longer photoperiod, it is interesting to determine whether or not, by migrating to a higher latitude to breed, these species could obtain a better summer energy balance. To answer this question a migration schedule was postulated similar to that of the dickcissel, *Spiza americana,* which is a winter resident in Panama and northern South America and a summer resident in central Illinois. Potential, existence and productive energy for the months of May through August were calculated for each species on the basis of mean monthly temperatures and photoperiods at Champaign, Illinois. Since average summer photoperiods in Illinois do not quite reach 15 hours, values were interpolated on the basis of the relative distance of the mean monthly photoperiod between regression lines for 12 and 15 hours at the mean temperature of the month.

Figure 3 shows graphically the relationship between the values for the variable seedeater in winter in Panama and in summer in Illinois. Throughout the summer, potential energy is greater in Illinois than in the Canal Zone because of the longer photoperiods. Existence energy is also greater, especially during early and late summer. Productive energy is well below the Canal Zone

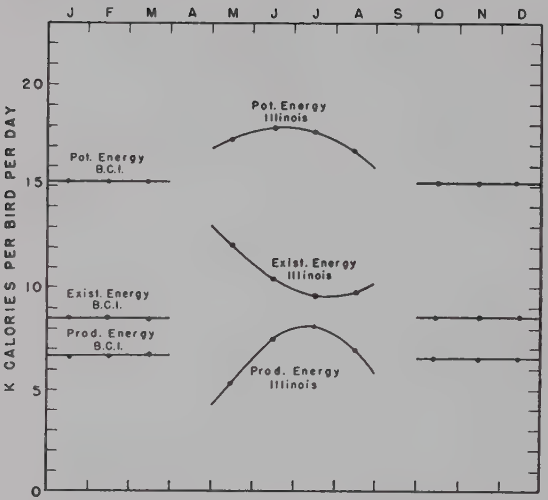

FIG. 3. Potential, existence, and productive energy for the variable seedeater at Barro Colorado Island during the winter and in Illinois during the summer.

level in early and late summer, and is equal to or above the level in the Canal Zone for a period of only about 2½ months.

Over the entire summer, existence requirements in Illinois were 24.6-31.8% greater for the variable seedeater, green-backed sparrow and blue-black grassquit, while productive energy averaged only 2.5-7.0% greater (Table XIV). Thus, the small increase in productive energy is at a cost of a relatively large increase in existence energy.

TABLE XIV. Comparison of existence and productive energy (kcal/bird day*) in the Canal Zone and at Champaign, Illinois during the summer (May-Aug.)

	Variable seedeater	Blue-black grassquit	Green-backed sparrow
Existence energy			
Illinois..........	10.499	9.106	0.501
Canal Zone......	8.423	6.935	0.380
Percent greater in Illinois.......	24.6	31.3	31.8
Productive energy			
Illinois..........	6.944	6.585	0.430
Canal Zone......	6.775	6.223	0.402
Percent greater in Illinois.......	2.5	5.8	7.0

* kcal/g bodyweight for the green-backed sparrow.

The early part of the summer, when productive energy is low, corresponds to the period of territory formation and pairing in nesting migratory species. These are important parts of the reproductive cycle, and a low level of productive energy could be critical. In general, it can be said that little advantage would be gained by migration, since the increased level of productive energy is small, and is present for only part of the summer.

It should be noted that migration to areas in the southern United States where summer temperatures are equal to or above those of the Canal Zone could provide the species with an energy balance more favorable than that at Barro Colorado Island.

The preceding analysis is, of course, not intended to show the critical reason why the species are not migratory, but only to indicate whether or not their energy balance would allow a migratory pattern to be developed. A complete discussion of factors preventing the development of migration would require both the analysis of the overall fitness of the environment in a given area and the consideration of hazards of the migratory movements.

Unfavorable energy balance may limit distribution in another way. As the range of resident species extends progressively farther from the equator, the winter daylength becomes shorter. In the present study it has been shown that daylength affects energy balance, with the more favorable balance occurring at the longer photoperiod. Thus, it is possible that at short daylengths (9-10 hrs) and lower winter temperatures, maximum ability to metabolize energy may fall below the energy requirements for existence. This may be a factor limiting the ranges of some of the species studied. For example, at 33°S latitude the blue-black grassquit, a permanent resident, encounters winter conditions of a 10-hour daylength and mean temperatures of 14.2°C during the coldest month. If the reduction in potential energy between 12 and 10 hours is proportional to that between 15 and 12 hours, this value would be reduced from 13.158 kcal/day at 12 hours to 11.050 kcal/day at 10 hours (Figure 4). In the same manner existence energy at 14.2°C would be reduced from 10.245 kcal at 12 hours to 9.257 kcal at 10 hours. Maximum metabolized energy under these conditions would be only 1.793 kcal above existence energy. From this rough analysis it is apparent that existence requirements may approach the maximum limits of metabolism under these conditions, especially during periods of colder than average weather.

SUMMARY

Measurements of the energy requirements for existence were made for 4 resident tropical finches at 12- and 15-hour photoperiods and temperatures ranging from +4.4° to +38.9°C at Barro Colorado Island, Panama Canal Zone, from February

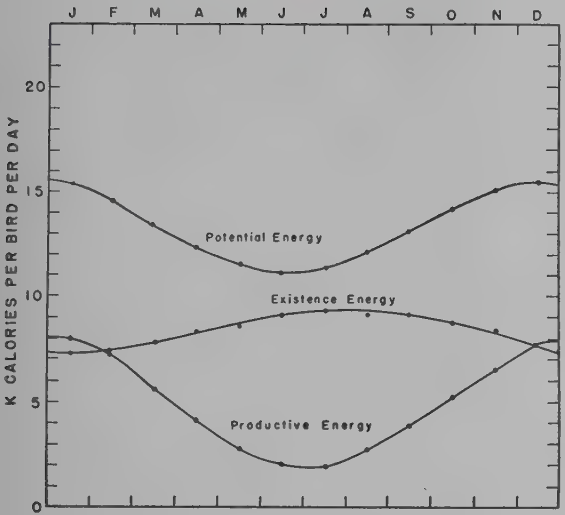

FIG. 4. Calculated energy balance of the blue-black grassquit through the year at 33°S latitude.

8 to September 15, 1959. Species used were the variable seedeater, *Sporophila aurita,* yellow-bellied seedeater, *S. nigricollis,* blue-black grassquit, *Volatinia jacarina,* and the green-backed sparrow, *Arremonops conirostris.*

Under experimental conditions no significant differences were observed in body weights at the 2 photoperiods. Weights increased significantly at low temperatures and decreased significantly at high temperatures. In the variable seedeater, heavier birds tended to metabolize more on a per bird basis but not on a per gram bodyweight basis.

Gross energy intake increased linearly with decreasing temperature. Intake was greater at the longer photoperiod and showed a greater rate of increase with decrease in temperature.

There was no significant variation in caloric value per gram excrement with temperature or photoperiod. Energy loss in the excrement increased linearly with decreasing temperature. Excretory energy per gram bodyweight was greater at the 15-hour photoperiod and showed a greater rate of increase with decrease in temperature. Execretory energy loss per hour of daylight was lower on the longer photoperiod.

Efficiency of food utilization tended to increase with increasing temperatures. In the variable seedeater, efficiency at 15 hours remained high at lower temperatures than at 12 hours.

Metabolized energy increased linearly with decreasing temperature. The level was significantly higher and the rate of increase with temperature greater on the 15-hour photoperiod. Metabolized energy intake per hour of light was lower at the 15-hour photoperiod.

Low limits of temperature tolerance for the variable seedeater, yellow-bellied seedeater, and blue-black grassquit were 2.8°C at 12 hours and 0°C at 15 hours. For the green-backed sparrow, limits were about —7.4°C at both daylengths. High limits of temperature tolerance at 12 hours were 38.9°C for the variable seedeater and green-backed sparrow, 40.6°C for the yellow-bellied seedeater, and 42.2°C for the blue-black grassquit. At 15 hours, limits were 41.7°C for the variable seedeater and green-backed sparrow, and 43.9°C for the yellow-bellied seedeater and blue-black grassquit.

Yearly variation in temperature and photoperiod at Barro Colorado Island is small, but well marked dry and wet seasons occur. Ranges of the species studied extend 20-33 degrees from the equator, where all encounter greater fluctuations of temperature and photoperiod than in the Canal Zone. Breeding seasons and periods of molt typically occur during times of the year when food is most available and the least amount of energy need be expended in obtaining it.

Calculated productive energy increased linearly with increasing temperature to about 35°C and at each temperature was greater at the 15-hour photoperiod. The levels of potential, existence, and productive energy of wild birds remain nearly constant during the year in the Canal Zone.

In these species, the advantages that would be gained by migration to the latitude of central Illinois for a summer breeding season are small, since the slight increase in productive energy would be available for only part of the summer and at a cost of a considerable increase in energy required for existence. Limits of distribution as permanent residents may be set at high latitudes by the maximum ability for metabolizing energy on the short photoperiods falling below requirements for existence at the low winter temperatures.

REFERENCES

Davis, E. A., Jr. 1955. Seasonal changes in the energy balance of the English sparrow. Auk **72**: 385-411.

Dixon, W. J. and F. J. Massey, Jr. 1957. Introduction to statistical analysis. New York, McGraw-Hill.

Eisenmann, Eugene. 1952. Annotated list of birds of Barro Colorado Island, Panama Canal Zone. Smithsonian Misc. Coll., vol. 117, no. 5.

Hellmayr, C. E. 1938. Catalogue of the birds of the Americas. Field Mus. Nat. Hist., Zool. Ser. 13, pt. XI.

Kendeigh, S. C. 1949. Effect of temperature and season on energy resources of the English sparrow. Auk **66**: 113-127.

Odum, E. P. 1959. Lipid deposition in nocturnal migrant birds. Proc. XII Int. Ornith. Cong.

Ostle, Bernard. 1954. Statistics in research. Ames, Iowa State College Press.

Siebert, H. C. 1949. Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. Auk **66**: 128-153.

Skutch, Alexander. 1954. Life histories of Central American birds. Pacific Coast Avifauna, No. 31.

Smithsonian Institution. 1951. Smithsonian meteorological tables, sixth revised edition. Smithsonian Misc. Coll., vol. 114.

U. S. Department of Commerce. 1959. World weather records, 1941-50. Washington, U. S. Government Printing Office.

West, G. C. 1958. Seasonal variation in energy balance of the tree sparrow in relation to migration. Ph.D. thesis, University of Illinois.

POPULATION DYNAMICS OF SOME FRESHWATER ZOOPLANKTON[1]

Donald H. Hazelwood and Richard A. Parker
Washington State University, Pullman

Introduction

Purpose and scope

The study of a natural population in its environment requires a careful evaluation of the interrelationships between the population and the biological, chemical, and physical factors of the environment. Cladocerans, in particular *Daphnia*, along with copepods, provide ideal populations for study since they are found in almost any body of fresh water during the spring and summer. These entomostracans are subject to extreme fluctuations in density, the causes of which are not adequately understood. Most previous studies have dealt with the role of a single environmental factor in regulating a planktonic population. Here it will be assumed that there is a complex of environmental factors responsible for population fluctuation. It is the intent of this paper to evaluate each seemingly important factor with proper regard for the simultaneous action of the remaining factors.

The effects of various environmental factors upon these zooplankters have been evaluated by many investigators. Birge (1898) suggested that temperature determined the reproductive rhythm and was the major factor in determining the total numbers of entomostraca in Lake Mendota. This was supported by Ward (1940) and Pratt (1943). Coker (1933) and Aycock (1942) studied the effect of temperature on size of *Cyclops*. Coker and Addlestone (1938) and Brooks (1946) have discounted the direct effect of temperature on cyclomorphosis in *Daphnia* except possibly during its embryonic period, while Brooks (1947) and Hrbáček (1959) have studied the effect of turbulence on cyclomorphosis. Kiang (1942) found that head height in 2 species of *Daphnia* was directly related to temperature in some lakes.

The relationships between phytoplankton and zooplankton have been studied by Hardy and Gunther (1935), Harvey *et al.* (1935) and Pennington (1941). Pennak (1946, 1949) suggests that no correlation exists between algal populations and zooplankton, whereas work by Cheatum *et al.* (1942) and Anderson *et al.* (1955) indicates that a possible correlation does exist. Comita and Anderson (1959) found a highly significant correlation between chlorophyll concentration and *Diaptomus* egg production. Ryther (1954) has shown that the growth, reproduction and survival of *Daphnia magna* are inhibited by senescent *Chlorella*. Banta *et al.* (1939), Slobodkin (1954), and Slobodkin and Richman (1956) have found a direct relatoinship between total food available and reproduction and growth. Slobodkin (1954) also found that interval of feeding was related to number and size of the animals. Borecky (1956) has concluded that densities of Cladocera are primarily determined by food supply and show a significant correlation with the physical and chemical factors related to food supply.

Green (1955, 1956) and Hoshi (1949, 1957a, 1957b, 1959) have studied the effect of dissolved oxygen concentration upon oxygen consumption, haemoglobin content, and heart-beat rate of certain Cladocera. MacArthur and Baillie (1926, 1927, 1929a, 1929b) have investigated the effects of various temperatures upon metabolic activity and duration of life of *Daphnia magna*. Richman (1958) and Slobodkin (1959) dealt with the energetics of *Daphnia pulex;* the former finding that the caloric value of the animal increases with development, while the latter computed the true efficiency of growth.

---

[1] This investigation was supported in part by a Summer Fellowship for Graduate Teaching Assistants from the National Science Foundation, a Predoctoral Fellowship from the National Institutes of Health, United States Public Health Service, and a National Science Foundation Research Grant G-8911. Material presented here was taken from a thesis to be submitted by the senior author in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Washington State University. The cooperation of Wilbert A. Rodgers, Manager, Turnbull National Wildlife Refuge, is gratefully acknowledged.

Relatively little work has been done on the various aspects of intraspecies and interspecies competition; however, Frank (1952) has found that when 2 cladocerans, *Daphnia* and *Simocephalus,* occupy the same medium, the latter is eliminated. Parker (1960) found a marked depression of *Cyclops* numbers when reared with *Simocephalus.*

Parker (1959) reported on the effect of 2 extremes in photoperiod (continuous light and continuous dark) on the reproduction of *Simocephalus.* Stephens (1955) and Stephens (1952) have shown an influence of photoperiod on molting and gonadal development of crayfish. Possibly their results are applicable, in part, to the entomostracans considered here.

Description of Kepple Lake

Kepple Lake, the site of this study, is located in the Turnbull National Wildlife Refuge in northeastern Washington.

This area was originally a shallow marsh with a meadow border. About 1910, it was drained by a series of ditches for agricultural purposes. The refuge was officially established in 1937, with Kepple Lake being formed behind an earthen dam in 1941. Because of its limited drainage area, it required about 10 years to bring it up to its present status. It now provides nesting and protective areas for migratory waterfowl.

The average depth of the lake is 2 meters and its very irregular surface ($D_L = 2.8$), surrounded by open *Pinus ponderosa* forest, covers an area of 32.3 hectares. The lake is essentially divided into 2 narrowly connected basins oriented in a northeast-southwest direction. Sampling was primarily confined to the northeast basin which comprises approximately two-thirds of the total surface area. The water is relatively clear (effective light extinction coefficient approximately 1.5) except during the *Aphanizomenon flos-aquae* bloom during June and July. Water temperatures are generally high throughout the summer with a maximum of 26.8°C in July and the pH is always above 7.0. The lake is of the seepage type with the only outlet being a dam spillway in the southwest corner. This spillway was effective only during the spring. Throughout the summer and fall, the water level of the lake gradually fell because of evaporation thus causing the alkalinity steadily to increase.

The bottom of the lake is covered with a dense growth of *Myriophyllum* and *Chara.* Although there are no fish in the lake, *Chrysemys picta* and the larvae of *Ambystoma tigrinum, A. macrodactylum, Rana pretiosa, Bufo boreas,* and *Hyla regilla* are common.

Description of Zooplankton

Daphnia schødleri and *Diaptomus leptopus* were by far the most common species found. Only rarely (on the order of a few per 100 liters) were *Cyclops* or *Ceridaphina* encountered in the samples. The authors are indebted to J. L. Brooks for the identification of the *Daphnia* and to G. W. Comita and M. S. Wilson for identification of the *Diaptomus.* For descriptions of these species see Brooks (1957) and Ward and Whipple (1959).

As a result of overlapping generations it is virtually impossible to calculate life cycle duration for *Daphnia schødleri* from field data. However, based on laboratory studies, it would appear that the duration is on the order of 6 to 8 weeks under low temperatures and short photoperiods, and less than 2 weeks under midsummer temperatures and photoperiods.

The average number of eggs per gravid female ranged from 2 to 14, the former occurring in midsummer and the latter preceding the spring and fall population peaks. The average number of eggs per liter was inversely related to fecundity.

D. schødleri males were found in small numbers during March, July, September, October and November. The greatest densities, 2.0 and 1.7/l, occurred on July 2 (week 14) and September 17 (week 25), respectively.

As for *Diaptomus leptopus,* field studies by us subsequent to the work reported here show a mean life cycle duration of 5.2 weeks during the spring and summer. Under laboratory conditions, G. W. Comita and J. A. Munro (personal correspondence) found the duration of the nauplier stages to be 10 to 12 days, and of the copepodid stages to be approximately 25 days.

The average number of eggs per sac ranged from 22 to 78, with the minimum occurring during the summer, and the maximum during the spring and fall. The mean number of egg sacs per liter ranged from 0.0 to 24.4, with the lowest numbers occurring from January through April and during August, September and December. The greatest numbers occurred during May, June, July, October and November.

METHODS

Sampling

Forty weekly samples taken at 0.5 meter during the period March 1959 to March 1960 were analyzed for densities of zooplankton, effective light extinction, possible food, water temperature, dissolved oxygen, and total alkalinity. Photoperiod and linear time trends were also considered. Sampling was done at the same time and on the same day of each week except on a few occasions. Fig-

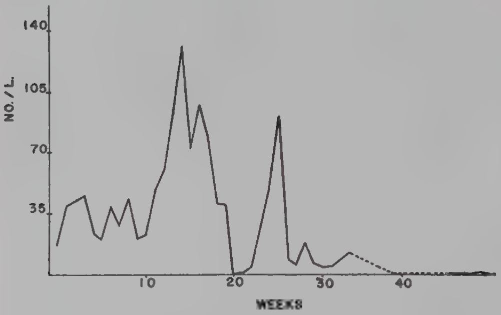

FIG. 1. Number of *Daphnia schødleri*/liter in Kepple Lake, Washington, during the period March 1959 to March 1960.

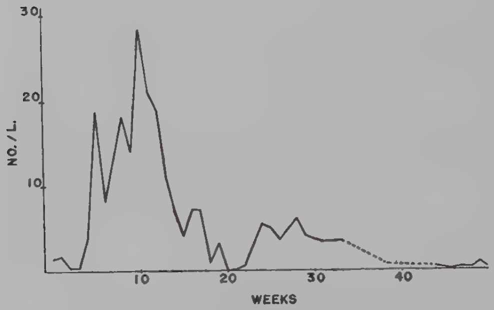

FIG. 2. Number of *Diaptomus leptopus*/liter in Kepple Lake, Washington, during the period March 1959 to March 1960.

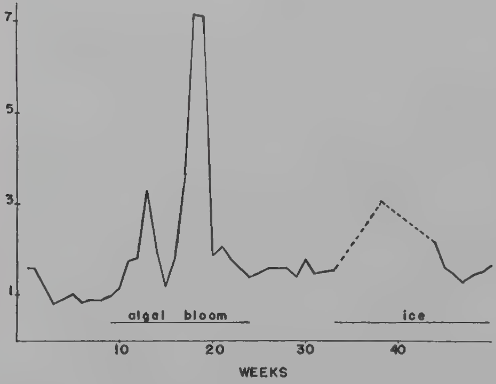

FIG. 3. Effective light extinction coefficient in Kepple Lake, Washington, during the period March 1959 to March 1960.

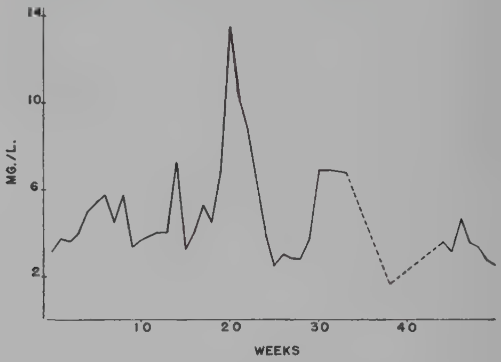

FIG. 4. Possible food (mg/1) in Kepple Lake, Washington, during the period March 1959 to March 1960.

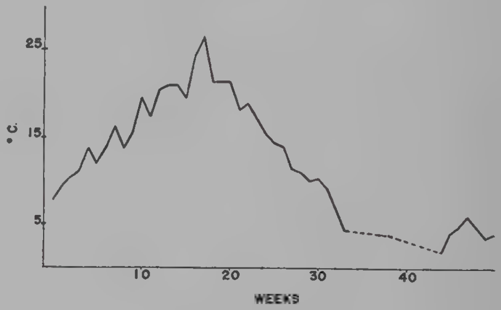

FIG. 5. Temperature (°C) in Kepple Lake, Washington, during the period March 1959 to March 1960.

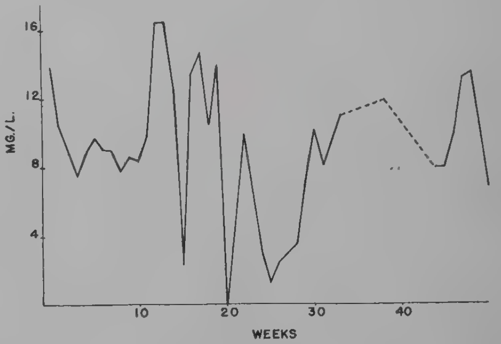

FIG. 6. Dissolved oxygen (mg/1) in Kepple Lake, Washington, during the period March 1959 to March 1960.

ures 1-8 show the seasonal variation of each factor considered.

A Clark Bumpus plankton sampler with a number 2 silk bolting cloth net was utilized. Only the nauplier stages of *Diaptomus* were missed because of the coarseness of the net. The sampler was calibrated at 4.0 liters of water per revolution. Samples were preserved in 3% formalin. Each concentrated sample was then diluted to a known volume (usually 400 ml). Ten one ml sub-samples were taken from the above by means of a 1 cc Foerst piston pipette and the number of zooplank-

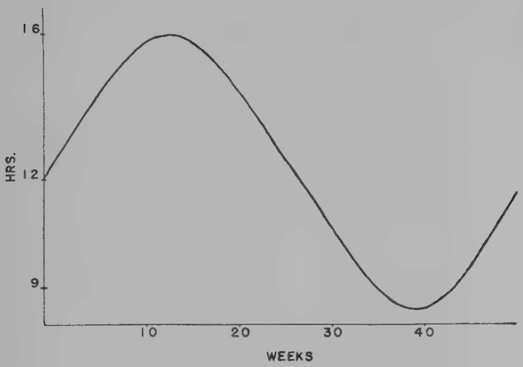

FIG. 7. Photoperiod (hrs) at Kepple Lake, Washington, during the period March 1959 to March 1960.

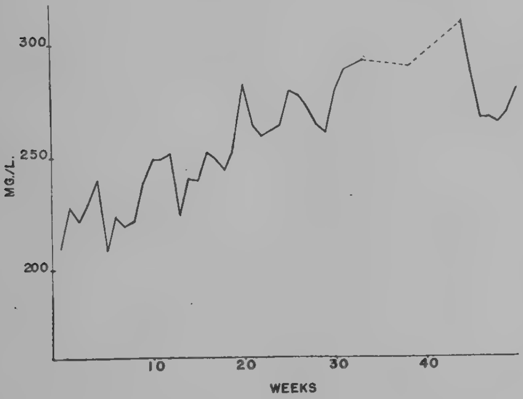

FIG. 8. Total alkalinity (mg/1) in Kepple Lake, Washington, during the period March 1959 to March 1960.

ton recorded. The number per liter per sample was then computed by the following equation:

$$n = \frac{(\text{average of the 10 subsamples})\ (\text{ml dilution})}{4\ (\text{revolutions of sample})}$$

See Fig. 1 and Fig. 2.

Light transmission was measured with a Whitney Underwater Light meter. From the empirical formula, $I_z = I_0 e^{-\eta z}$, and the method of least squares, the best estimate of the effective extinction coefficient ($\hat{\eta}$) was computed. See Fig. 3.

Water samples, taken with a modified Kemmerer sampler, were strained through number 25 silk bolting cloth which has a mesh diameter of approximately 60 μ. The water was then filtered through HA Millipore filters with a pore diameter of 0.45 ± 0.02 μ. It was estimated by gut measurements of *Daphnia* and *Diaptomus* that all particles within the above range (0.45-60μ) could be ingested. After Millipore filtration, the filters were dried in a vacuum oven at 40°C for 24 hours. Each filter was then weighed on a Gram-atic Semi-Micro Balance (Fisher #1-911). A higher drying temperature was not used since the filters themselves tended to lose weight. The dry weight of material per liter of water was then computed and used as an estimate of possible food for the zooplankton. All material within the above-mentioned range was included because of work by Pennak (1946) who reported that a major portion of zooplankton food appears to consist of detritus. Lebour (1922) found bits of copepods mixed with other debris in the guts of *Calanus,* and that in the lab, organic debris seemed to be the main food. Dakin (1908) and Woltereck (1908), as reported in Esterley (1916), concluded that nannoplankton was the most important food item for copepods and cladocerans, respectively. Järnefelt (1940) included tripton as a decisive part of the diet of microcrustaceans and cites Knauthe (1907), Naumann (1918) and Rylov (1931) in support of this. See Fig. 4.

Temperature measurements were made by use of a Whitney Underwater Thermometer, Model TC5. Thermal stratification never occurred because of the shallowness of the lake. See Fig. 5.

Oxygen samples were taken and concentrations were determined by the Winkler method. Checks were made for the presence of interfering substances but none were found. See Fig. 6.

Photoperiods were computed from sunrise to sunset tables in the Air Almanac, U. S. Naval Observatory, for each day of observation. See Fig. 7.

Total alkalinity as expressed in concentrations of carbonate and bicarbonate ions was determined by the standard phenophthalein-methyl orange titration (Welch 1948). See Fig. 8.

Almost every biological system incorporates time as an element, that is, the number of organisms present in a certain environment determines to some extent the number that will be present at a future date. As a result there is a mutual dependence of successive samples due to time trends. If this dependence is linear, then by including it as a variable in the regression analysis, it is possible to remove its effect.

Analysis of data

It is very difficult to evaluate the interrelationships of the various environmental factors either for simultaneous effects or for lag effects by conventional methods. The use of simple correlations in such problems could be very deceiving since the correlation between any 2 factors might be due to the influence of one or more of the other factors rather than to the interrelationship between the 2 themselves. For these reasons techniques of partial correlation and multiple regression were employed. The method of partial correlation eliminates the effects of those factors which, through their common relationship to the factors to be correlated, bias the true correlation. In other words, partial correlation is nothing more than the degree of relationship between 2 variables holding all other influencing factors at a "fixed" level. If no other factors are involved, then the partial correlation reduces to the simple correlation. An example of this influence, as cited in Richardson (1944), is as follows:

> Let 1 represent the carpal area of children,
> 2 represent the mental age of children, and
> 3 represent the chronological age of children.
>
> The following simple correlations were obtained: $r_{12} = 0.83$, $r_{13} = 0.92$, $r_{23} = 0.88$.
>
> Note the apparent high correlation between carpal area and mental age of children. However, if we eliminate the common relation of chronological age to the other two variables, we get
>
> $$r_{12.3} = 0.11$$
>
> which indicates very little, if any, correlation.

For a theoretical treatment the reader is referred to Kendall (1945), Cramér (1946), and Tintner (1952).

RESULTS AND DISCUSSION

The analyses were made on a week to week basis thus yielding "simultaneous" correlations. Such correlations may not give a "true" picture of the relationship between the variables, as will be noted below, since normally an environmental factor exerts its effect at some later time. To determine such "true" correlations, it is necessary to introduce lag into the observations. Since several sampling dates were missed, time lags and auto correlation could not be considered. However, the analysis as presented indicates the overall effects throughout the study period.

The results are summarized in Table I with number of *Daphnia*/liter as the dependent variable, and in Table II with number of *Diaptomus*/liter as the dependent variable. Each table contains 3 sets of values as follows: simple correlations, partial correlations and regression coefficients for the regression analysis excluding time as a factor, and partial correlations and regression coefficients for the regression analysis including time as a factor. Since the same data have been utilized for more than one regression, significance considerations are unjustified; however, probability values have been noted beneath each set of values to aid in interpretation of the results.

Density of Diaptomus *and density of* Daphnia

The negative effect between number of *Diaptomus*/l and number of *Daphnia*/l indicates what might be considered as interspecific competition. On the basis of these results alone, there is no indication as to which species is dominant. However, Frank (1952) reported that *Daphnia pulicaria* (= *D. pulex;* see Brooks 1957) caused the extinction of *Simocephalus vetulus* when reared together under laboratory conditions. Parker (1960) noted a marked depression in numbers of *Cyclops viridis* when reared with *Simocephalus vetulus.* He employed rank correlations and determined that the maximum negative correlation occurred with 7 weeks lag, concluding that *Simocephalus* seems to interfere with the normal development of *Cyclops* in such a way that future fecundity is reduced.

TABLE I. Correlations and regression coefficients associated with number of *Daphnia*/liter and factors analyzed

Factor	No.	Simple	Partial					
			Excl. Time			Incl. Time		
		r_{1i}	$r_{1i.}$	$b_{1i.}$	Probability	$r_{1i.}$	$b_{1i.}$	Probability
Daphnia/liter	1	—	—			—		
Diaptomus/liter	2	.316	−.286	−1.28	0.10	−.306	−1.39	0.08
Effective light extinction	3	.150	−.254	−5.32	0.15	−.250	−5.19	0.16
Possible food	4	−.065	−.480	−5.76	0.01	−.493	−6.03	0.01
Temperature	5	.657	.376	3.53	0.03	.333	3.18	0.06
Oxygen	6	.220	.287	1.82	0.10	.311	2.04	0.08
Photoperiod	7	.661	.161	5.28	0.35	.177	5.82	0.32
Total alkalinity	8	−.431	.070	0.11	0.70	.141	0.29	0.44
Time	9	−.496	—			−.131	−0.39	0.47
Coef. of Multiple Correlation			.788		0.01	.792		0.01
Unbiased Standard Error of Estimate			22.99			23.16		
Regression Equation Constant			−84.28			−126.50		

TABLE II. Correlations and regression coefficients associated with number of *Diaptomus*/liter and factors analyzed

Factor	No.	Simple	Partial					
			Excl. Time			Incl. Time		
		r_{21}	$r_{21.}$	$b_{21.}$	Probability	$r_{21.}$	$b_{21.}$	Probability
Daphnia/liter	1	.316	−.286	−0.06	0.10	−.306	−0.07	0.08
Diaptomus/liter	2	—	—			—		
Effective light extinction	3	−.182	−.397	−1.87	0.02	−.384	−1.76	0.03
Possible food	4	−.099	−.378	−1.02	0.02	−.410	−1.10	0.02
Temperature	5	.414	.026	0.05	0.90	−.026	−0.05	0.90
Oxygen	6	.147	.306	0.43	0.08	.351	0.51	0.05
Photoperiod	7	.596	.451	3.31	0.01	.467	3.38	0.01
Total alkalinity	8	−.419	.275	0.09	0.12	.348	0.16	0.05
Time	9	−.476	—			−.224	−0.15	0.20
Coef. of Multiple Correlation			.750		0.01	.765		0.01
Unbiased Standard Error of Estimate			5.15			5.10		
Regression Equation Constant			−55.52			−69.12		

Effective light extinction

Little relationship was found between effective light extinction and number of *Daphnia*/l, whereas a very high negative correlation was found with number of *Diaptomus*/l. The latter implies that the amount of light transmitted through the water in some way affects *Diaptomus* reproduction; that is, the smaller the attenuation of light waves through the water, the greater the reproduction in the copepods. In view of the above, it would be advisable to consider the effect of intensity at different wave lengths in future studies.

Possible food

The number of *Daphnia*/l appears to be highly correlated with possible food and this in a negative fashion ($r_{14} = -.493$). However, if one considers the effects of a large population of zooplankters upon the quantity of phytoplankton and detritus, it would seem that the relationship between the 2 at any time would be of a negative sign. This negative effect has been postulated by many investigators. Hardy and Gunther (1935) and Harvey *et al.* (1935) both reported that "grazing" by herbivorous zooplankton was sufficient to control the population of phytoplankton. Pennington (1941) reported a cyclic sequence of events in laboratory experiments in which she relates the reproductive rate of the phytoplankton to the number eaten by the zooplankton. Anderson *et al.* (1955) observed compatible results in 2 lakes in Washington, in that the zooplankton populations were greatest during periods of phytoplankton minima. They concluded that "grazing" by zooplankton was the best possible explanation. As stated previously, Borecky (1956) concluded that densities of Cladocera were primarily determined by food supply.

A high negative correlation was also found between possible food and number of *Diaptomus*/l, possibly for the same reasons expressed above. Comita and Anderson (1959) reported a highly significant simple correlation of 0.598 between chlorophyll concentration and the mean number of eggs/sac in *Diaptomus ashlandi.* Marshall and Orr (1958) concluded that egg laying in *Calamus finmarchicus* depended upon food supply.

Temperature

Water temperature appears to be well correlated with density of *Daphnia.* Temperatures ranged from a minimum of 2.0°C in January to a maximum of 26.8°C in July. The lake was nearly isothermal on every observation date, but no evidence of cyclomorphism occurred. The positive relationship obtained is in good agreement with the results of some investigators. Birge (1898) and Ward (1940) both concluded that temperature was the most important single physical factor in determining sizes of entomostracan populations. On the other hand, Pratt (1943) found that the population size of *Daphnia magna* at 18°C was 2½ times that at 25°C. Slobokin (1954) found a similar relationship for *Daphnia obtussa* (= *D. parvula;* see Brooks 1957), and suggested that it might result from energy expenditure by the animals at the higher temperatures.

There appears to be no correlation between temperature and density of *Diaptomus.* However, Coker (1933) and Aycock (1942) found that *Cyclops* reared at low temperatures were larger in size than those reared at high temperatures. Aycock also reported that there was a higher mortality rate in the low temperature group. Raymont (1959) found an increase in respiratory rate with an increase in temperature.

Oxygen

Dissolved oxygen concentration is positively correlated with density of *Daphnia.* Examination of Fig. 1 and Fig. 6 does not appear to substantiate this relationship, since large densities of *Daphnia* were observed at both high and low oxygen concentrations. However, from Parker and Hazelwood (unpublished) it appears that the minimal concentration necessary for survival of *Daphnia* is approximately 1 mg/l. Since this concentration was exceeded on all but one date (week 20) it would appear that oxygen has a positive influence on such factors as natality and survival of young which would in turn influence population size. Density of *Diaptomus* is also well correlated with oxygen.

It should be noted that on August 13 (week 20) the oxygen content was zero at all depths in the northeast basin of the lake, but not in the southwest basin. Because of this, 4 equally spaced 0.5 meter samples were taken starting at the southwestern end and proceeding toward the northeastern end of the lake. The results are given below.

Station	Oxygen (mg/1)	*Daphnia*/l	*Diaptomus*/l
1	2.5	120.4	11.6
2	2.2	55.8	3.1
3	1.3	0.2	0.1
4	0.0	0.0	0.0

The rapid increase in numbers of zooplankton (especially the daphnid) in the weeks following can be explained in part by the above, and also by the possibility of oxygen sufficient micro-habitats existing along the shoreline enabling the zooplankters to survive while the center of the basin was devoid of dissolved oxygen.

Photoperiod

There is little correlation of photoperiod with density of *Daphnia;* however, there is a real positive correlation with density of *Diaptomus*. Parker (1959) found under laboratory conditions a positive effect of continuous light on reproductive rate as evidenced by numbers of *Simocephalus* juveniles present. Since algal food appeared to be in excess in all cultures, it was assumed that the smaller population developing in continuous darkness was not due to a lower food supply. Stephens (1952) reported that the duration of photoperiod did not appear to influence the frequency of the oöcyte cycle in *Cambarus,* but it did have a direct influence on the amplitude of the cycle. Stephens (1955) found that *Cambarus* fails to molt in continuous darkness and that the tendency to molt increases with increasing day length. He also noted a significant increase in mortality with longer photoperiods.

Total alkalinity

No correlation appears to exist between total alkalinity and density of *Daphnia,* where as a positive correlation exists with density of *Diaptomus*. Ward (1940) reports no correlation of carbonate concentration with entomostracan populations, but suggests that pH acts as a slight limiting factor to some of these animals. On the other hand, Borecky (1956) reported a highly significant positive correlation between total Cladocera density and bicarbonate concentration. Whittaker and Fairbanks (1958) state that copepods are excluded from lakes of high salinity.

Time

There appears to be little correlation between time and density of *Daphnia* or *Diaptomus*. This implies that either there is little relationship between linear time trend and the animals studied, or that the relationship is of a more complex nature than that of linearity. For example, the relationship might be sinusoidal as shown by Stephens (1952) in *Cambarus* oöcyte formation, maturation and resorption. Consideration of Tables I and II indicate that linear time contributes only slightly to the analysis.

Coefficient of multiple correlation

The high multiple correlations found indicate that good relationships exist between the dependent variables and the factors considered; in other words, there is a good closeness of fit of the regression equations to the observed values of the dependent variables. Correcting for numbers of samples and variables, the percentages of variation accounted for amount to 53 and 48 for the daphnid and the diaptomid, respectively. The variation not accounted for might be due to some of the trace elements (*e.g.,* chromium, iron, strontium, and vanadium) found in the water, or to some of the organisms that prey on entomostracans. These factors are being considered in present studies.

SUMMARY

1. Weekly samples taken during the period March 1959 to March 1960 from Kepple Lake, Washington, were analyzed for number of *Daphnia*/l, number of *Diaptomus*/l, effective light extinction, possible food, water temperature, dissolved oxygen and total alkalinity. Photoperiod and linear time trend were also considered.

2. Multiple regression-partial correlation techniques were applied to the data. Autocorrelation and time lags were not considered since sampling date intervals were not always constant.

3. Number of *Daphnia*/l is correlated with possible food, and to a lesser extent with number of

Diaptomus/l, water temperature and dissolved oxygen.

4. Number of *Diaptomus*/l is correlated with photoperiod, possible food, effective light extinction, dissolved oxygen, and total alkalinity, and to a lesser extent with number of *Daphnia*/l.

REFERENCES

Anderson, G. C., G. W. Comita, and V. Engstron-Heg. 1955. A note on the phytoplankton-zooplankton relationships in two lakes in Washington. Ecology **36**: 757-759.

Aycock, D. 1942. Influence of temperature on size and and form of *Cyclops vernalis* Forbes. Jour. Elisha Mitchell Sci. Soc. **58**: 84-93.

Banta, A. M., L. A. Brown, and L. Ingle. 1939. Studies on the physiology, genetics, and evolution of some Cladocera. Carnegie Inst. Wash. Dept. Genetics Paper No. 39.

Birge, G. A. 1898. Plankton studies on Lake Mendota. II. Crustacea of plankton from July, 1894 to December, 1896. Trans. Wis. Acad. **11**: 274-448.

Borecky, G. W. 1956. Population density of the limnetic Cladocera of Pymatuning Reservoir. Ecology **37**: 719-727.

Brooks, J. L. 1946. Cyclomorphosis in *Daphnia*. I. An analysis of *D. retrocurva* and *D. galata*. Ecol. Monog. **16**: 409-447.

———. 1947. Turbulence as an environmental determinant of relative growth in *Daphnia*. Proc. Nat. Acad. Sci. **33**: 141-148.

———. 1957. The systematics of North American *Daphnia*. Memoirs Conn. Acad. Sci. **13**: 180 pp.

Cheatum, E. P., M. Longenecker, and A. Metler. 1942. Limnological observations on an east Texas lake. Trans. Amer. Microsc. Soc. **61**: 336-348.

Coker, R. G. 1933. Influence of temperature on size of fresh-water copepods (*Cyclops*). Int. Rev. Hydrobiol. **29**: 406-436.

——— **and H. H. Addlestone.** 1938. Influence of temperature on cyclomorphosis of *Daphnia longispina*. Jour. Elisha Mitchell Sci. Soc. **54**: 45-75.

Comita, G. W. and G. C. Anderson. 1959. The seasonal development of a population of *Diaptomus ashlandi* Marsh, and related phytoplankton cycles in Lake Washington. Limnol. Oceanogr. **4**: 37-52.

Cramér, H. 1946. Mathematical methods of statistics. Princeton, Princeton Univ. Press.

Dakin, W. J. 1908. Notes on the alimentary canal and food of Copepoda. Int. Rev. Hydrobiol. **1**: 772-782.

Esterley, C. O. 1916. The feeding habits and food of pelagic copepods and the question of nutrition by organic substances in solution in the water. Univ. of Cal. Pub. Zool. **16**: 171-184.

Frank, P. W. 1952. A laboratory study of the intraspecies and interspecies competition in *Daphnia pulcaria* and *Simocephalus vetulus*. Physiol. Zool. **25**: 178-204.

Green, J. 1955. Haemoglobin in the fat-cells of *Daphnia*. Quant. J. Micr. Sci. **96**: 173-176.

———. 1956. Variation in the haemoglobin content in *Daphnia*. Proc. Roy. Soc. B **145**: 214-232.

Hardy, A. C. and E. R. Gunther. 1935. The plankton of the South Georgia whaling grounds and adjacent waters. Discovery Reports **11**: 1-456.

Harvey, H. W., L. H. N. Cooper, M. V. Lebour, and F. S. Russell. 1935. Plankton production and its control. Jour. Mar. Biol. Assoc. U. K. **20**: 407-422.

Hoshi, T. 1949. Studies on physiology and ecology of plankton. II. Oxygen consumption and heart beat rate in developmental stages of *Simocephalus vetulus* O. F. Muller). Sci. Rep. Tohoku Univ., Sec. 4 (Biol.) **18**: 59.

———. 1957a. Studies on physiology and ecology of plankton. XII. Changes in oxygen consumption of the daphnid, *Simocephalus vetulus*, with the decrease of oxygen concentration. Sci. Rep. Tohoku Univ., Ser. 4 (Biol.) **23**: 27-33.

———. 1957b. Studies on physiology and ecology of plankton. XIII. Haemoglobin and its role in the respiration of the daphnid, *Simocephalus vetulus*. Sci. Rep. Tohoku Univ., Ser. 4 (Biol.) **23**: 35-58.

———. 1959. Studies on physiology and ecology of plankton. XIV. Critical respiration for the dissociation of oxygen from haemoglobin of the daphnid, *Simocephalus vetulus*. Sci. Rep. Tohoku Univ., Ser. 4 (Biol.) **25**: 239-245.

Hrbáček, J. 1959. Circulation of water as a major factor influencing the development of helmets in *Daphnia cucullata* Sars. Hydrobiologia **13**: 170-185.

Järnefelt, H. 1940. Ein kleiner Beitrag zur Triptonfrage. Arch. Hydrobiol. **36**: 319-329.

Kendall, M. G. 1945. The advanced theory of statistics. Vol. 1. N. Y., Hafner.

Kiang, G. H. 1942. Über die Cyclomorphose der Daphnien einiger Voralpenseen. Int. Rev. Hydrobiol. **41**: 345-408.

Knauthe, K. 1907. Das Süsswasser. Neudamm.

Lebour, M. V. 1922. The food of plankton organisms. J. Mar. Biol. Assoc. U. K. **12**: 644-677.

MacArthur, J. W. and W. H. T. Baillie. 1926. Sex differences in mortality and metabolic activity in *Daphnia magna*. Science, N. S. **64**: 229-230.

———. 1927. Relations between metabolism, longevity, and sex in *Daphnia magna* as expressed at different temperatures. Anat. Rec. **37**: 146-147.

———. 1929a. Metabolic activity and duration of life. I. Influence of temperature on longevity of *Daphnia magna*. Jour Exp. Zool. **53**: 221-242.

———. 1929b. Metabolic activity and duration of life. II. Metabolic rates and their relation to longevity in *Daphnia magna*. Jour. Exp. Zool. **53**: 243-268.

Marshall, S. M. and A. P. Orr. 1958. On the biology of *Calanus finmarchicus*. X. Seasonal changes in oxygen consumption. J. Mar. Biol. Assoc. U. K. **34**: 459-472.

Naumann, E. 1918. Über die natürliche Nahrung des limnischen Zooplanktons. Lunds Univ. Arsskr. N. F. Avd. **2**: 14.

Parker, R. A. 1959. *Simocephalus* reproduction and illumination. Ecology **40**: 514.

———. 1960. Competition between *Simocephalus vetulus* and *Cyclops viridis*. Limnol. Oceanogr. **5**: 180-189.

Pennak, R. W. 1946. The dynamics of fresh-water plankton populations. Ecol. Monogr. **16**: 339-355.

———. 1949. Annual limnological cycles in some Colorado reservoir lakes. Ecol. Monogr. **19**: 233-267.

Pennington, W. 1941. The control of the numbers of fresh-water phytoplankton by small invertebrate animals. J. Ecol. **29**: 204-211.

Pratt, D. M. 1943. Analysis of population development in *Daphnia* at different temperatures. Biol. Bull. **85**: 116-140.

Raymont, J. E. G. 1959. The respiration of some planktonic Copepods. III. The oxygen requirements of some American species. Limnol. Oceanogr. **4**: 479-491.

Richardson, C. H. 1944. An introduction to statistical analysis. N. Y., Harcourt, Brace and Co.

Richman, S. 1958. The transformation of energy by *Daphnia pulex*. Ecol. Monogr. **28**: 273-291.

Rylov, W. 1931. Über das Tripton-Problem. Verhandl. d. I. V. L., 5.

Ryther, J. H. 1954. Inhibitory effects of phytoplankton upon the feeding of *Daphnia magna* with reference to growth, reproduction, and survival. Ecology **35**: 522-533.

Slobodkin, L. B. 1954. Population dynamics in *Daphnia obtusa* Kurz. Ecol. Monogr. **24**: 69-88.

———. 1959. Energetics in *Daphnia pulex* populations. Ecology **40**: 232-243.

——— **and S. Richman.** 1956. The effect of removal of fixed percentages of the newborn on size and variability of *Daphnia pulicaria* (Forbes) populations. Limnol. Oceanogr. **1**: 209-237.

Stephens, G. J. 1952. Mechanisms regulating the reproductive cycle in the crayfish, *Cambarus*. I. The female cycle. Physiol. Zool. **25**: 70-84.

Stephens, G. C. 1955. Induction of molting in the crayfish, *Cambarus*, by modification of daily photoperiod. Biol. Bull. **108**: 235-241.

Tintner, G. 1952. Econometrics. N. Y., John Wiley and Sons.

Ward, E. B. 1940. A seasonal population study of pond Entomostraca in the Cincinnati region. Amer. Midl. Nat. **23**: 635-691.

Ward, H. B. and G. C. Whipple. 1959. Fresh-water biology. 2nd ed. N. Y., John Wiley and Sons.

Welch, P. S. 1948. Limnological methods. Philadelphia, Blakiston.

Whittaker, R. H. and C. W. Fairbanks. 1958. A study of plankton copepod communities in the Columbia Basin, southeastern Washington. Ecology **39**: 46-65.

Woltereck, R. 1908. Hydrobiologische Notizen. II. Die natürliche Nahrung pelagischen Cladoceran und die Rolle des "Zentrifugenplanktons" in Süsswasser. Int. Rev. Hydrobiol. **1**: 871-874.

REPRODUCTIVE ECOLOGY AND SOUND PRODUCTION OF THE TOADFISH, *OPSANUS TAU*[1]

Grace-Ann Gray and Howard E. Winn
Zoology Department, University of Maryland, College Park

Introduction

The fact that fishes produce a variety of sounds has been clearly demonstrated in recent years (e.g. Fish 1954). These sounds are made under a variety of behavioral circumstances, yet few studies have been made of their functional significance. The toadfish, *Opsanus tau* (Linnaeus), was selected for studies on sound and its relation to breeding biology because it is known to produce 2 distinctly different sounds. Also, these fish nest in shallow water where they are accessible to observation and experimentation. The objective of this study is to describe the reproductive biology of the toadfish and at the same time to attempt to analyze the relationship of sound production to the behavior of the fish.

General descriptions of the life history of *Opsanus tau* have been published by Ryder (1886), Gill (1907), and Gudger (1910). They have pointed out that the toadfish utilizes old cans, jars, and the undersides of various other solid objects as nests which the males defend in the late spring and early summer in northern latitudes. The female enters the nest to deposit eggs on the underside of the object and then leaves. It has usually been assumed that in Chesapeake Bay the eggs hatch in 10 to 15 days and that the larvae remain hanging by a pedicel for another 3 to 4 weeks. Gudger (1910) stated that the diet of *O. tau* varies with the habitat, and noted that the blue crab is eaten most frequently, whereas Hildebrand and Schroeder (1928) claimed the fish to be omnivorous.

It has been known for many years that *O. tau* makes a harsh grunt and a more musical sound referred to as the boatwhistle call (Gill 1907). Sorensen (1884), Tower (1908), and Fish (1954) identified the air bladder as the organ of sound production and they demonstrated that contraction of the muscles attached to each side of the air bladder results in emission of the grunt. More intensive studies have been made in recent years where the sounds have been analyzed for their frequency, time, harmonic, and intensity characteristics (Fish *et al.* 1952, Fish 1954, Fish *et al.* 1959, Tavolga 1958b). Fish (1954) associated the boat-whistle call with prespawning and early egg-guarding activity, and because of this the sound was referred to vaguely as a mating call. On morphological grounds it was thought that both

---

[1] This is contribution No. 13 of the Chesapeake Bay Fund, Zoology Department, University of Maryland.

sexes could produce the boat-whistle and it was claimed that the grunt was produced throughout the year by both sexes (Fish 1954). Tavolga (1958b) compared the physical characteristics of sounds produced by *Opsanus tau* and *O. beta* (Goode and Bean), whereas Fish and Mowbray (1959) analyzed sounds emitted by a West Indian form, *Opsanus sp.* According to Knudsen *et al.* (1948) the boat-whistle call was not subject to any diurnal variation.

MATERIALS AND METHODS

Most observations and all experiments were made in the shallow water beside the long pier at the Chesapeake Biological Laboratory, Solomons, Maryland, during the late spring and early summer of 1958 and 1959. The pier which was 6 feet wide served as a permanent location of testing areas and facilitated the placement of the equipment. From the dock a hydrophone could be placed directly over or beside a nest. The water depth along the dock varied from 0 to 12 feet but the area utilized in this study was 2 to 5 feet deep.

Tin cans and glass jars, open at one end (17.5 cm in length by 10.5 cm in diameter and 21.7 cm by 15.6 cm), were utilized as nests by the toadfish. These were placed at intervals of 10 feet along each side of the pier. Seventy-three nest containers were studied during each year. In 1958, 5 cans were placed in the water on June 17, 12 on June 18, 26 on June 29, 24 on July 1, and 6 glass containers on July 16. In 1959, all 73 containers were placed in the water on or before May 22.

At the onset of the 1958 testing program, some males were removed from the cans, sexed by means of the external urogenital papillae, measured, marked with numbered strap-tags (small mammal ear tags) on the left operculum and returned to the water. All of the tagged fish left the area so that in 1959 individuals were recognized by the distinctive characteristics of the fleshy projections around the mouth and eyes. On occasion, these were clipped underwater while the fish were still in the cans. Sex was determined on a different occasion.

Data were collected on the length of time males stayed at a nest, the time it took the eggs to hatch and the time the young remained in the cling stage. If the nests were checked every 24 hours this resulted in a range of 48 hours in any of the data, since the eggs were laid at an unknown time within a 24-hour period and hatched at an unknown time within a 24-hour period. For example, if no eggs were found in a particular nest on July 8 but were present on July 9, and the eggs were still there on July 15 but were cling young on July 16, then the hatching time was recorded as between 6 and 8 days. If the time between checks was greater than one day, the range would be greater.

One hundred and thirty-five specimens, collected in crab pots, were sexed by examination of the gonads in order to verify the reliability of the use of the urogenital papillae for the determination of sex. This method was 100% reliable with reproductively mature fish. The male papilla was smooth, round, and somewhat elongated, whereas the female papilla was short, swollen, irregular, and red in appearance.

In 1958, the recording equipment consisted of a Tandberg Tape Recorder (Model 3BF) and a Tandberg crystal microphone (flat response between 30 and 12,000 cps in air) waterproofed with a rubber membrane. In 1959, a Magnemite Portable Tape Recorder (Model 610DV) was used in conjunction with a hydrophone (Model LF-310A-A) equipped with an internal preamplifier.

The first underwater recordings of sound were made on June 24, 1958, after spawning had started and were continued until August 20 at which time all spawning and sound production in the study area had ceased. In 1959, intensive listening and recording began on May 22 when spawning had already begun and observations were continued until September 9. Data on sound production by various males in their nests were kept throughout these periods.

In order further to understand the behavior of a male at its nest in the various phases of reproduction (with and without eggs or young) a series of presentation tests were made in 1958 and 1959. The items presented were: male toadfish (either normal, anaesthetized, or confined in a jar); female toadfish with ovulated eggs; blue crabs, *Callinectes sapidus* Rathbun, 4 to 5 inches in carapace width; adult bloodworms, not from the Chesapeake Bay, *Polycirrus eximius* (Leidy); menhaden, *Brevoortia tyrannus* (Latrobe), 4 to 6 inches in total length; and oyster shells. These objects were tied to a dark-colored fish line and placed before a male in its nest. Sound recordings and visual observations of 50 seconds duration were made for each presentation experiment.

In 1959 four wire pens, 15 by 15 feet, were constructed of one-inch square heavy welded wire and placed along the pier. These pens permitted the study of known individual fish.

RESULTS

Data on the reproductive seasons of 1958 and 1959 are presented in Table I, where information is given on the number of nests that were empty or occupied, as well as whether or not there were eggs, young free from the egg but still attached

Table I. A resumé of the condition of the toadfish nest containers and their occupants during the spawning season beside the Solomons Island Laboratory dock during 1958 and 1959

Nest Condition	May	June											July														August							Sept.
	29	8	15	16	18	22	23	24	25	26	29	30	1	2	3	7	8	10	15	16	17	23	24	27	28	30	4	5	6	11	13	17	18	4
1958[a]																																		
Total empty					4			8	8	9		29	25	49	44	48			57	58		64	67		64	61		62						
Total occupied					1			9	9	8		14	18	18	23	19			10	9		9	6		9	12		11						
Single fish[b]					1			6	7	5		2	7	5	16	16			7	4		4	2		3	6		8						
Pair of fish					0			2	2	1		12	7	7	1	0			0	0		1	0		0	0		0						
Pair & eggs					0			0	0	2		0	2	0	1	0			0	0		0	0		0	0		0						
Male & eggs					0			1	0	0		0	2	6	5	3			2	4		1	1		2	2		1						
Male & cling young					0			0	0	0		0	0	0	0	0			1	1		3	3		4	2		1						
Male & free young					0			0	0	0		0	0	0	0	0			0	0		0	0		0	2		1						
1959[a]																																		
Total empty	46	45	41	40	45	40	42		39	43	43	43	43	47	55		57	60	61		63	63		65		68	70		67	63	68	64	64	66
Total occupied	27	28	32	33	28	33	31		34	30	30	30	30	26	18		16	13	12		10	10		8		5	3		6	10	5	9	9	7
Single fish[b]	7	4	5	3	2	11	8		7	2	2	2	1	3	2		4	0	0		0	2		3		2	1		6	10	5	9	9	7
Pair of fish	0	3	5	1	0	1	3		0	0	0	1	1	1	0		2	1	0		1	0		0		0	0		0	0	0	0	0	0
Pair & eggs	1	1	0	2	0	0	0		0	2	0	0	0	0	0		0	0	0		0	0		0		0	0		0	0	0	0	0	0
Male & eggs	19	18	12	12	11	5	5		12	10	12	10	13	9	6		0	2	2		1	0		0		0	0		0	0	0	0	0	0
Male & cling young	0	2	10	15	15	16	14		15	14	8	9	8	9	7		8	8	6		5	5		3		1	0		0	0	0	0	0	0
Male & free young	0	0	0	0	0	0	1		1	2	8	8	7	4	3		2	2	4		3	3		2		2	2		0	0	0	0	0	0

[a] See materials and methods for the date of placement of nest cans.
[b] These single fish were usually males.

to the nest by a pedicel (cling young), or detached free-swimming young. Additionally, eggs were not located on May 8, 1959, but on May 22 there were many cans which contained either a pair or a male with freshly laid eggs. The data (Table I) demonstrate that maximum reproductive activity occurred throughout the month of June and the first part of July. Actual spawning began in late May and usually was completed by early August. Based on the presence of eggs, the 1959 spawning season was several weeks longer than in 1958. The reduced number of cling young and attached young during 1958 were caused by manipulation of the nest cans.

In Table II data are presented on the sex ratios of some toadfish caught in crab pots in 1958. Although the data are extremely limited, the male catch from June 29 to July 20 suggested that most of the males were on nests and that the low catch of females represented a time when many were spawning. Early in July, the catch of females increased and this was correlated with the fact that most of the females had already laid their eggs. As the males began to leave the nests in large numbers at the end of July, the catch of males increased and was about equal to the number of females caught from July 27 to August 3. A progressive increase in the number of spent females was evident (Table II).

In the nests studied (Table I) a female spawned with a male in a can, and as soon as a clutch of eggs was deposited she left the immediate area and went into either beds of vegetation or deeper water. A male in a can usually received eggs from a single female. The males maintained residence in the cans until the young had attained the free-swimming stage. Twenty-nine fish, found in cans, proved to be males when sexed either by examination of the gonads or the urogenital papillae.

Table II. The sex ratio and sexual condition of females of *Opsanus tau* captured in crab pots placed at Little Cove Point, 1½ miles southeast of Drum Point Light during the breeding season of 1958

Date	Numbers of Individuals			
	Male	Female		
		Ripe	Spent	Total
June 15	1	5	2	7
June 22	11	5	3	8
June 29	3	1	0	1
July 6	0	1	0	1
July 13	8	2	17	19
July 20	3	1	8	9
July 27	10	0	10	10
Aug. 3	23	0	21	21

The males without eggs moved freely throughout the area and from can to can until they received eggs. Males with eggs or young also left, but less readily. Thirty-five fish that were strap-tagged in 1958 left their shelters or nests (24 were individual males, 10 were members of a pair and one was a male with eggs). Eight single males, seven with eggs, one with cling young, and four with detached young left their shelter or nest after they were handled during the 1958 season. Two males, one with eggs and one with detached young, had returned to their cans by the next day. When objects were presented to males in nests (experiments to be discussed later), 20 males in cans without eggs, 3 in cans with eggs and one with cling young left the area and only one returned to its container. Nine males in 1959, identified individually by the fleshy projections around the head, were noticed in separate cans without eggs or young on one day, but were not there when the cans were checked one to 2 days later. One returned 4 to 7 days later to his original can and remained to receive eggs.

From periodic inspection of the nests (Table I) it was possible to obtain information on the length of time a male stayed in a nest. Marked males that were followed from the time a pair entered the nest until free young were present, stayed for at least 23, 25, 25, 36, and 37 days, whereas 4 unmarked fish stayed for at least 24, 28, 28, and 37 days. In all instances it was not known how long these males remained with the free young except where 2 unmarked individuals stayed a total of 31 to 36 and 32 to 37 days with the eggs and young. Other marked and unmarked males, in attendance at the nest from the egg to the free young stage, were studied, but the exact date of egg-laying and the length of stay with the young were unknown. The data were as follows (in minimum number of days): 20, 21, 22, 26, 27, 33, 33, 34, 35, 35, 37, and 46. It appeared as though the males usually stayed with the eggs, cling young and free young from 23 to 46 days, although, under other conditions of temperature, this time may be shorter or longer. The length of stay also appeared to be affected by disturbances.

The time that it takes the eggs to hatch was based on the following data: 6-8, 6-9, 6-9, 7-9, 6-8, 5-7, 7-12, 9-11, 9-11, 8-10, 7-9, and 8-10 days. The first 7 hatching times occurred between June 23 and July 3, 1959, whereas the next 3 times occurred between June 15 and 26. The shorter hatching times of the first group were correlated with high temperatures (Figure 1). The egg-hatching periods varied from 5 to 12 days. The data for the length of the cling stage in days were as follows: 4-6, 6-9, 9-11, 9-11, 9-16, 10-14, 10-17, 11-15, 11-15, 12-14, 14-16, 14-17, 15-23, 15-24, and 19-27. The first 2 times, which seemed significantly shorter than the others, occurred during the temperature peak of late June, 1959 (Figure 1). A salinity plot exhibited no obvious correlation. It appears as though the cling stage usually varied from 6 to 19 days with a potential range of 4 to 27 days. A figure of 9 to 15 days seemed to be more normal during the time of this study. The male stayed with the young in 4 instances from 5-6, 6-7, 7-18, and 10-15 days. This time was quite variable because the male readily left the container when disturbed.

The toadfish make grunt-like sounds when they are taken out of the water and handled. These also may be heard when a swimmer or another male toadfish approaches a male in a nest cavity. In order to test which kinds of stimuli evoked a grunt response from a male, a variety of objects was presented to males in various phases of the reproductive cycle. The responses of the fish are summarized in Table III. A male on his nest nearly always grunted at active male toadfish and he grunted somewhat less than 50% of the time at females and inactive males. However, inactive

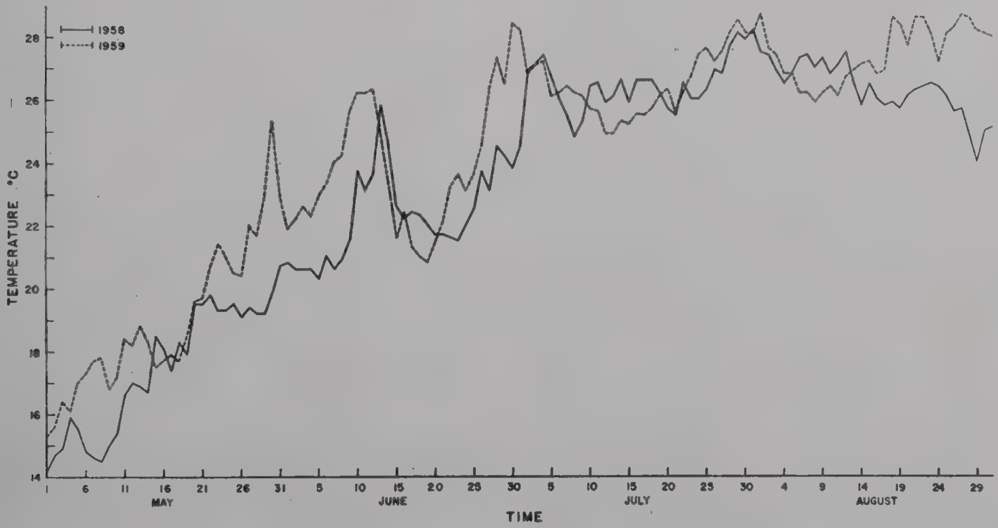

FIG. 1. Surface temperatures at the end of the pier, Chesapeake Biological Laboratory, Solomons, Maryland.

TABLE III. Grunt and attack responses of nest-guarding male toadfishes toward a variety of objects

Introduced material	Nest-guarding male toadfish with:	Number of tests	Responses					
			Grunt			Attack		
			Yes	No	% that grunted	Yes	No	% that attacked
Oyster shells..........	Eggs & young	22	2	20	9	2	20	9
	None present	22	0	22	0	6	16	27
Bloodworms..........	Eggs & young	3	0	3	0	3	0	100
	None present	2	0	2	0	1	1	50
Blue crabs............	Eggs & young	37	15	22	41	28	9	76
	None present	23	0	23	0	16	7	70
Menhaden............	Eggs & young	10	0	10	0	4	6	40
	None present	1	0	1	0	0	1	0
Ripe female toadfish...	Eggs & young	33	13	20	39	5	28	15
	None present	13[1]	5	8	36	1	13	7
Active male toadfish...	Eggs & young	50	43	7	86	16	34	32
	None present	36	27	9	75	5	31	14
Inactive male toadfish[2].	Eggs & young	27	12	15	44	0	27	0
	None present	21	2	19	9	0	21	0

[1] Three individuals (9 tests) not included, responded with a boat-whistle call—see text.
[2] Includes fish, anesthetized or confined in a jar.

males appeared to cause fewer grunts from males with no eggs or young. Attacks were infrequent or absent with toadfish as the stimulus. When such objects as menhaden, bloodworms, and oyster shells were present, a grunt response was usually not evoked but it was frequently produced when crabs were placed in front of males guarding eggs or young. Attacks (or feeding responses) were frequent toward menhaden, blue crabs, and bloodworms. The oyster shells elicited a small percentage of attacks. Thus toadfish, especially active males, were the stimuli that elicited the maximum production of grunt responses. Males with eggs and young either grunted or attacked more frequently than males without eggs or young. This was further substantiated by the fact that in 20 tests males without eggs and young left the can at the start of an experiment (thus no response, and therefore not included in Table III, whereas only 3 males with eggs deserted their nests).

In an unusual circumstance many grunts were produced by several fish. On July 31, 1959, an underwater explosion occurred about 5 miles from the pier while underwater sound recordings were being made beyond the pier in water 30 feet deep. As soon as the sound of the explosion was heard, several toadfish emitted a series of grunts for several seconds.

Another sound produced by the toadfish is referred to as the boat-whistle call. Twenty individuals that emitted boat-whistles in cans or other cavities were all males. Many other toadfish (48 plus) that produced this sound were believed to be males on the basis that only males have been found to stay in the nest and guard the eggs. Not once was a female found that emitted the boat-whistle in the large area surrounding the pier. A particular effort was made to listen over females in the area. Several wire pens were placed in the water beside the dock and no sound was heard from 4 females in one pen, whereas in another pen the one male present emitted boat-whistles. In a 3rd pen one pair and a single male with eggs were present, and boat-whistle calls were heard only piror to the removal of the males.

During 1958, boat-whistles were heard from June 18 when the work began until July 15 when the call became infrequent. Finally, none of these sounds was heard from July 28 to August 12. No sounds were heard from toadfish known to be around the dock when checked for 45 minutes on November 7, 1958, 70 minutes on March 27, 1959, and over 15 minutes on April 25, 1959. On May 8, 1959, a few calls were heard that did not seem to represent the regular boat-whistle or the usual grunt but appeared to be some precursor to the usual boat-whistle call. On May 22 many odd grunts or short boat-whistles and one regular boat-whistle were heard and a few cans contained freshly laid eggs. From May 24 through early June many of these sounds were produced. They then decreased in frequency until none was heard from July 30 to September 4, 1959. Although no boat-whistles were heard at these times in the experimental area, they were prevalent from July 28, in water 30 feet deep located straight out from the laboratory pier, until August 18, after which date they were no longer produced.

Boat-whistles were heard from 39 males on nests without eggs, from 8 with eggs, and from one with cling young, and in no instance from a male with free young. In 22 of the 39 instances, when a lone male in the can produced boat-whistles, the male stayed in the same can and received eggs shortly thereafter.

In 46 experiments (Table III) where ripe female toadfish were presented to males with and without eggs or young, the male in over 50% of the cases made no observable reaction, whereas in somewhat less than 40% a grunt response was given. However, a different response was obtained in 9 experiments not included in Table III, as follows: On July 15, 1958, in 4 experiments when a live ripe female on the end of a string was moved past a silent male in a jar without eggs, he responded with a series of boat-whistles. This was repeated on July 24 with the same results and eggs were laid in the jar between July 24 and July 28. In a similar experiment on June 24, 1959 the male, which was boat-whistling earlier in the day, responded with a rapid series of boat-whistles after which the female entered the can. The same experiment was repeated later in the day and the male again responded with boat-whistles. Similarly in an experiment on the same day with another male, which was boat-whistling, the response was the production of a more rapid series of the same sound. The female then entered the can and turned upside-down. This was repeated later in the day and the male again responded with an increased rate of sound production.

Discussion

The previously published information on the reproductive season of *Opsanus tau* is sketchy and there is a lack of evidence that anyone has determined the first egg-laying date for any population or that anyone has systematically checked nests throughout an entire reproductive season. Furthermore, local differences in shallow water and deep water populations and yearly climatic differences might be expected, particularly if temperature is causative. Based on several years records, Gudger (1910) stated that at Woods Hole, Massachusetts, eggs and young were found in June, July and August. The earliest recorded dates were June 3 and June 12. Other data from Woods Hole which are in disagreement are given as follows: spawning occurred in the month of June only, and freshly laid eggs were rarely found in July; eggs or young were found in June, July and August, and oviposition occurred about the middle of July (various references in Gudger, 1910). Gill (1907) found eggs on July 14 and young on July 21 at Noank, Connecticut, whereas Fish (1954) concluded that eggs were not laid until at least after the middle of June in Wickford Harbor, Rhode Island. Nichols and Breder (1926) gave June and July as the spawning months in the vicinity of New York City. Hildebrand and Schroeder (1928) stated that in the Chesapeake Bay, spawning apparently took place throughout the summer, as females with large eggs were taken from April 13 to October 25, 1922 (note that this did not state ripe eggs). Gudger (1910) found advanced embryos the first week in June and eggs in segmentation late in August in the Beaufort, North Carolina area and maintained that the higher temperatures at Beaufort allowed the breeding season to be drawn out. Gill (1907) said that in the southern states, the approach to shore and the reproductive season commenced in April or May in the Gulf of Mexico (a different species as the group is now understood). Breder (1941) stated that reproduction took place when the water temperature reached its approximate maximum, whereas, in the southern form, reproduction took place when it reached its approximate minimum. He further stated that these fish spawned for the most part in water in the middle and high sixties (°F) extending, where the temperature rise was rapid, into the seventies or even the low eighties. Breder gave the spawning season for *O. beta* at Palmetto Key on the west coast of Florida as February and March.

Our data for one local shallow water population of toadfish demonstrated that eggs were laid in water temperatures from 63.5°F (17.5°C) or slightly below to 80°F (27°C) or higher (compare egg-laying dates with Figure 1), and that this period extended from between May 8 and 22 to between July 10 and 15, 1959. Males with cling and free young were found up to August 6, 1959. The fact that boat-whistles were heard in deeper water until August 18, 1959, is interpreted to mean that individual males still may have been ripe and may have been guarding eggs in early stages of development. It seems obvious that there are inadequate data for a comparison among Atlantic Coast populations, but it is reasonable to assume that spawning occurs earlier in the southern part of the range. Certainly, Breder (1941) demonstrated that *O. beta* spawned in February and March, but whether or not they also layed eggs earlier was not clearly documented. On the basis of sound production and observation of our population we presume that the boat-whistling of *O. tau* in late August near St. Augustine and the first hooting of *O. beta* heard on August 20, 1957 on the west coast of Florida (Tavolga 1958b) represented the onset of reproductive activity. There was some evidence that 1958 reproduction of the Solomons Island population was slightly more protracted because eggs were found at least 15 days later than in 1959 (Table I).

In essence, the results are in agreement with previous authors on the following points. The male guards the nest and stays with the young for a short time after they are free in the nest (Gudger 1910, Breder 1941). The nest is a can, jar, under a shell, board or other object, and the eggs are attached to the roof, usually in a single layer (*e.g.* Gudger 1910, Ryder 1887). The fish are polygamous (*op. cit.*), although in most of our test cans only one clutch of eggs was deposited. This, in general substantiates Breder's (1941) statements that when nest materials are abundant there will be less chance that several females will deposit eggs in one nest. It is possible that a male without eggs is a more effective stimulus for the attraction of a female than a male guarding eggs and this would tend to reduce the number of clutches deposited in any one nest. This is supported by the fact that after eggs are deposited in a nest boat-whistles produced by the male become less frequent and soon disappear. Furthermore the small size of the cans may have limited the number of clutches. It was noticed that a few nests under large boards contained several clutches of eggs.

Various estimates have been made on the time it takes the eggs to hatch and the time it takes the cling young to free themselves as follows: At Woods Hole, Massachusetts, the fixed condition of the egg and embryo lasted for at least 3 to 4 weeks, and the egg-membrane was ruptured in about half that time (Ryder 1887), the cling stage lasted for 3 to 4 weeks (Clapp 1899), the eggs hatched in about 26 days while the young became free on the 42nd day, whereas at Beaufort, North Carolina, the egg burst the shell (now cling stage) 11 days after fertilization and the young stayed attached for 13 to 15 days (Gudger 1910). Again, as with the data on the reproductive season, it is impossible to tell how accurate these estimates are and there are certain conflicts in the information. It is difficult to rationalize a 26-day hatching period with information that eggs were not laid until at least the first or 2nd week of June in the Woods Hole area and were seldom or never found after the first of July. In summary, in the current study, eggs hatched in 5 to 12 days, the young usually remained clinging 6 to 19 days, and the male stayed with the free young 5 to 18 days. Most of the data were obtained from the middle of June to the end of July, and it is reasonable to assume that the incubation period is longer for eggs laid in late May when temperatures are lower. Although males move from can to can before the reception of eggs, once these are deposited the males stay for 25 to 46 days, as was established with marked individuals.

Many hypotheses have been formed in regard to the functions of sounds produced by fishes, but only Tavolga (1956, 1958a) has experimentally demonstrated the function of sound produced by a fish. He demonstrated that in combination with visual stimuli the short grunt made by male gobies during reproduction attracted the females. Potential functions of the 2 types of sounds emitted by the toadfish were postulated by Marie P. Fish (1954). She said that the grunt was no doubt a reaction to annoyance, fear and aggravation and might express both warning and alarm. She also presumed that the boat-whistle was some sort of mating call used only by individuals with mature sex products.

A primary stimulus to the production of the grunt is the approach of a male or unripe female toadfish. Except for the situation where blue crabs were introduced to a male with eggs, the grunt was usually not produced when food items were presented. The difference in the response to active and inactive males appears to be based on the difference in movement. The grunt is made less frequently by the male when he does not have young in the nest. Also it appears that toadfish outside of the breeding season and females ready to spawn are less prone to grunt than ripe males when handled. Thus a male guarding eggs has a greater internal stimulation to produce this call. It is reasonable to suppose that the grunt of a male on his nest is part of a stimulus situation that causes an approaching toadfish to leave the immediate vicinity of the nest.

The reaction to an introduced crab is less easily analyzed. Here is the only case where grunts were produced commonly when the presentation tests did not involve a male toadfish. Possibly in some manner the crab on approach to a nest is a stimulus situation that causes the guarding male to grunt and then bite the crab. There is no evidence that a crab can hear water-borne sound vibration. Whether this is primarily a food response or also an aggressive response is not amenable to analysis at this time. A food response, as well as supplying food, certainly prevents the crab from entering the nest. Fish (1954) referred to the crab as a natural enemy of the toadfish, but this is difficult to understand because the blue crab is an extremely common food item (Gudger 1910 and unpublished data).

In order to understand the potential functions of the boat-whistle sound, it was necessary to find out whether or not both sexes made this call. Fish (1954) said that since the air bladder was alike in both sexes and there was no apparent difference in their grunting, it seemed reasonable to believe that both male and female had the ability to produce this sound. But in the few cases where she located a sound producer, it was always a male. The data from the current study strongly suggest that only the male produces the boat-whistle call. There is no evidence to indicate that the female produced boat-whistles in the area studied. This is the first instance in fishes where, although only one sex makes the call, the sound producing apparatus is not structurally different.

Boat whistles were produced quite commonly throughout the shallow water area studied by us in constrast to their apparent rarity in the shallow waters of Wickford Harbor studied by Fish (1954). There is some indication that she did not listen early enough. This evidence that the boat-whistle is produced shortly before spawning and for a short time after the male has eggs, verifies Fish's statement that this call is associated with prespawning and early spawning activities.

A problem remains regarding the presence of boat-whistles in deeper water. Fish (1954) stated that throughout the prespawning period, before eggs were found in the shallow inlets of Wickford Harbor and nearby waters, a medley of boat-whistles arose from deeper water. Neither Fish (1954) nor Tavolga (1958b) have done more than listen to these sounds in deeper water. Possibly the fish produce these sounds just before migration to shallow water to nest as Fish suggested. It has been thought by most investigators that the toadfish move into deeper water in the winter. Although this is true for many individuals, we and personnel of the Solomons Island laboratory saw some toadfish during the winter in less than 10 feet of water off the dock in the study area. There is, of course, considerable movement into shallow water just before the spawning season. The underwater recordings demonstrated that when the fish first entered shallow water in May, 1959, the boat-whistle sound was uncommon but then became more frequent. Possibly the earlier calls in deeper water represent fish in nesting cavities ready to spawn with females. There is considerable movement of males from nest site to nest site until eggs are deposited and many males move into shallower water setting up various sites from which they call. There could be distinct deep water and shallow water populations wherein males of the deep water population mature several weeks earlier. In most instances in the animal kingdom, the male's sexual products are mature before eggs are ready for fertilization. This call is probably coincident with this maturation of the male's sperm although Tavolga (1958b) seems to think the call is also given when it has nothing to do with reproduction.

When ripe females were used as a stimulus, the male in his nest did not produce sound in over 50% of the experiments. Approximately 40% of the time grunts were emitted but in about 10% of the cases the males responded with a boat-whistle response. This was either by the production of the call (not previously emitted) or by an increase in the rate of sound production. It is possible to discount all the experiments (33 out of 46) where a ripe female was introduced to a male with eggs or young because most of the tests were conducted well after the middle of the reproductive season when most boat-whistling had discontinued. All of the 13 experiments were done with single males near the end of the spawning season (between June 29 and July 8, 1959, when most males had stopped calling; eggs were deposited in only one nest after June 29). Furthermore, a roughly handled female attached to a string and presented to a male on his nest might act abnormally. Also, the females that were utilized in the presentation tests might not have had ovulated eggs and thus might not represent the stimulus that elicits boat-whistling. On the basis of all the evidence, it would seem that boat-whistle emission in 9 instances is much more significant than the small number of responses would indicate.

The following is proposed as a working hypothesis: The boat-whistle call is given off by males at a nest when they are ready to spawn and this call is an attractive stimulus to females that are ready to lay eggs. The evidence to support this is as follows: only ripe males make the boat-whistle; this is emitted only from cavities; a male either starts to call or increases its rate when a ripe female is placed in front of the nest. In order to fully substantiate the above hypothesis, it will be necessary to find out more about the boat-whistle in deeper water and to carry out the critical playback experiments.

SUMMARY

The reproductive habits and sound production of a shallow water population of the toadfish, *Opsanus tau* (Linnaeus), were studied at Solomons Island, Maryland during June, July and August of 1958 and 1959.

Maximum reproductive activity occurred throughout the month of June and the first part of July. Crab-pot catches of the male and female toadfish were correlated with reproductive activities. The males guarded the nests from egg deposition until after the young were free swimming (23 to 46 days). Until eggs were deposited in a nest with the males, they apparently moved from object to object. In the population studied the eggs hatched in 5 to 12 days and the young remained in the cling stage 6 to 19 days.

Experiments with the grunt-like sound demonstrated that it was most frequently produced by a male in his nest when other males or spent female toadfish approached and especially so when eggs and young were present. Blue crabs occasionally would evoke the grunt response, but such objects as other species of fish, worms, and oyster shells were not adequate stimuli. It is suggested that ripe females and both sexes outside of the spawning season produced the grunt much less frequently.

Only the male produces the boat-whistle on the nest even though the structure of the sound producing apparatus is similar in both sexes. It is hypothesized that this call is a stimulus for the attraction of females to the nest. Data are presented which support this supposition, but it is emphasized that several critical experiments must still be performed.

ACKNOWLEDGMENTS

We wish to gratefully acknowledge the assistance of the following persons: Dr. L. Eugene Cronin, Director of the Chesapeake Biological Laboratory, for providing laboratory facilities; Dr. Frank Schwartz, Chesapeake Biological Laboratory, for his enthusiastic assistance; and Jane Goodrich, William Goodrich, John Stout, Joseph Marshall, Thomas Savage, and Anthony Picciolo for aid in conducting the presentation experiments. Mrs. Carolyn Winn kindly criticized the manuscript. Mr. Harten of Solomons Island generously supplied us with the toadfish used in dissections.

This study was supported by the Chesapeake Bay Fund, the U. S. Public Health Service, Institute of Neurological Diseases and Blindness (B-1668), and the Office of Naval Research (N.R. 104-489).

REFERENCES

Breder, C. M., Jr. 1941. On the reproduction of *Opsanus beta* Goode and Bean. Zoologica **26**: 229-232.

Clapp, C. M. 1899. The lateral line system of *Batrachus tau*. J. Morph. **15**: 223-264.

Fish, M. P. 1954. The character and significance of sound production among fishes of the western North Atlantic. Bull. Bingham Oceanogr. Coll. **14**: 1-109.

———**, A. S. Kelsey, Jr., and W. H. Mowbray.** 1952. Studies on the production of underwater sound by North Atlantic coastal fishes. J. Mar. Res. **11**: 180-193.

———**and W. H. Mowbray.** 1959. The production of underwater sound by *Opsanus sp.*, a new toadfish from Bimini, Bahamas. Zoologica **44**: 71-76.

Gill, T. N. 1907. Life histories of toadfishes (Batrachoidids), compared with those of weevers (Trachinids) and stargazers (Uranoscopids). Smithsonian Misc. Coll. **48**: 388-427.

Gudger, E. W. 1910. Habits and life history of the toadfish (*Opsanus tau*). Bull. U. S. Bur. Fish. (1908) **28**: 1071-1109.

Hildebrand, S. F. and W. C. Schroeder. 1928. Fishes of Chesapeake Bay. Bull. U. S. Bur. Fish. (1927) **43**: 337-338.

Knudsen, V. O., R. S. Alford and J. W. Emling. 1948. Underwater ambient noise. J. Mar. Res. **7**: 410-429.

Nichols, J. T. and C. M. Breder, Jr. 1926. The marine fishes of New York and southern New England. Zoologica **9**: 1-192.

Ryder, J. A. 1887. Preliminary notice of the development of the toadfish, *Batrachus tau*. Bull. U. S. Fish. Comm. (1886) **6**: 4-8.

Sorensen, W. 1884. Om Lydorganer hos Fiske. En physiologisk og comparative-anatomisk Undersgelse. Kjbenhavn: 245.

Tavolga, W. N. 1956. Visual, chemical, and sound stimuli as cues in the sex discriminatory behavior of the gobiid fish, *Bathygobius soporator*. Zoologica **41**: 49-64.

———. 1958a. The significance of underwater sounds produced by males of the gobiid fish, *Bathygobius soporator*. Phys. Zool. 31: 259-271.

———. 1958b Underwater sounds produced by two species of toadfish, *Opsanus tau* and *Opsanus beta*. Bull. Mar. Sci. of the Gulf and Caribbean **8**: 278-283.

Tower, R. W. 1908. The production of sound in the Drumfishes, the Sea-Robin and the Toadfish. Annals N. Y. Acad. Sci. **18**: 149-180.

THE CONTRIBUTION OF ALDER TREES (*ALNUS TENUIFOLIA*) TO THE PRIMARY PRODUCTIVITY OF CASTLE LAKE, CALIFORNIA

CHARLES R. GOLDMAN
University of California, Davis

INTRODUCTION

It is no longer enough to consider the lake as a microcosm in the sense proposed by Stephen A. Forbes (1887) in his classic and inspired paper. To understand the dynamics of a lake, careful thought must be given to a host of edaphic factors which influence the physical, chemical, and biological existence of the lake. Thienemann (1950) in reviewing the development of limnology notes that its main cultural significance as a science rests in the early stress placed on these interrelationships. The importance of organic matter contributed by inflowing streams or the accumulation of leaves has not been ignored (Reimer 1954). Because of the importance of nitrogen to the metabolism of a lake, the influence of nitrogen-fixing terrestrial plants is of special interest.

Although their nitrogen-fixing ability was unknown, interest in alder trees as a mysterious growth factor for other plants has existed for several centuries. Charles A. Johns (1849) noted in "Forest Trees of Britain" that "It has been observed that their shade is much less injurious to vegetation than that of other trees:

> 'The alder, whose fat shadow nourisheth—
> Each plant set neere to him long flourisheth.'
> —BROWNE."

This verse was quoted by Johns from *Britannia's Pastorals* (Book I, Song 2, line 357-8), a work written by William Browne of Tavistock in 1613. Since recognition that nodulated *Alnus glutinosa* grew better than the non-nodulated (Hiltner 1896), and the later proof that alder trees are non-leguminous nitrogen-fixing plants (Virtanen and Saastamoinen 1933, 1936, Bond *et al.* 1954, Virtanen *et al.* 1955), they have received a great deal of attention (Allen and Allen 1958).

My interest in alders as a significant nitrogen source for lakes was first aroused during studies on primary productivity and limiting factors in lakes of the Alaska Peninsula in 1957 (Goldman 1960a). During a period of limiting nitrogen levels the primary productivity of Brooks Lake, Alaska, increased significantly as one approached its major tributary. The source of nitrogen inflow could not be attributed to rainfall of the peninsula because it is unusually low in nitrogen. Similarly the volcanic ash which covered the Brooks Lake area following the Katmai eruption of 1913 is very nitrogen deficient. Alders on the Brooks Lake watershed appeared to be a likely source of nitrogen for the lake. Crocker and Major (1955) and Lawrence (1958) recognized the great importance of alder trees as a nitrogen source for other terrestrial plants in the glaciated areas of Alaska.

Although I was only able to speculate on the lake-alder relationship on the Alaska Peninsula in 1957, two years later I learned that Castle Lake, California, has a well developed stand of the mountain alder, *Alnus tenuifolia* Nutt., along the east shore with only a few isolated trees along the west shore (Figure 1). Examination of the roots of this species at Castle Lake showed them to have extensive nodule development. A study of factors limiting the lake's primary productivity was started in April 1959 which included the following evaluation of the alder trees' contribution to the fertility of the lake.

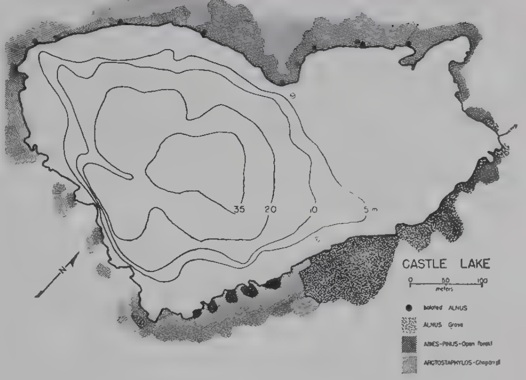

FIG. 1. Morphometric map of Castle Lake, California (Siskiyou County) indicating the distribution of the major vegetation forms.

Castle Lake is a moderately productive cirque lake of 19.46 ha (48 A) located in Siskiyou County, California T. 39 N., R. 5W., S 13. Trout production of this lake has been under investigation for many years and details of these investigations and description of the lake may be found in Wales (1946, 1947) and Wales and German (1956).

METHODS

To determine the relative accumulation of nitrogen on the east and west sides of Castle Lake, 21 soil auger samples, collected along both shores in 1959 and 1960, were placed in polyethylene bags, sealed, and quick frozen with dry ice. Eckman dredge samples of bottom sediment taken at a depth of 3 m on each side of the lake were treated in the same manner. These were stored frozen until analyzed on a dry weight basis for total Kjeldahl nitrogen (American Public Health Association *et al.* 1955) and inorganic nitrogen in extractible forms (NO_3^-, NO_2^-, NH_4^+) in the laboratory at Davis. Selenium was used as a catalyst in the Kjeldahl extractions. After aqueous extraction the phenoldisulfonic acid method of NO_3^- determination was used. Ammonia was determined by the semimicro distillation method after acidified sodium chloride extraction. Nitrite was determined using a colorimetric method (Rider and Mellon 1946). Water from springs along the east and west shore, lake water, and samples of the outflow stream were collected in polyethylene containers for colorimetric nitrogen analysis (NH_4^+, NO_2^-, NO_3^-) in the lake-side laboratory. Other samples were returned to Davis for flame spectrophotometric analysis.

Green leaves were picked from the alders and other deciduous trees in the area, quick frozen, and analyzed for % total organic nitrogen (Kjeldahl) on a dry weight basis as well as NO_3^- and NH_4^+. Several leaf-fall boxes were placed beneath the vegetation on both sides of the lake and their contents collected for analysis after defoliation in October. Samples of the terrestrial vegetation were collected and identified to indicate the general distribution of the major vegetation forms around the lake (Fig. 1).

To assess the actual effect of the springs draining the alder and non-alder sides of the lake on primary productivity, the rapid and sensitive C^{14} bioassay technique developed for detecting limiting factors *in situ* in Alaskan lakes (Goldman 1960a) was utilized. In these experiments untreated surface water collected from the middle of the lake in a 4 liter polyethylene bottle was divided into three 500 ml Pyrex culture flasks after inoculation with C^{14} (as sodium carbonate). All samples of spring water collected were HA Millipore filtered. Addition of 1% of the culture volume of the East Spring water was made to the first, West Spring water to the second, and distilled and demineralized water to the control. The cultures were maintained at lake surface light and temperature in a floating crib. Growth in the culture was measured by filtering aliquots of the cultures over a period of 8 days.

In conjunction with primary productivity work on the lake, simultaneous *in situ* measurements of photosynthetic carbon fixation were made at depths of 0, 1, 2, and 2.5 m of water 15 m from the East and West shore respectively. The sensitive C^{14} method (Steemann Nielsen 1952) as modified by Goldman (*ibid.*) was utilized for these measurements with dark bottle controls for assessing nonphotosynthetic uptake. Water samples were collected with a non-metallic sampler.

HA Millipore filters (porosity 0.45 ± .02 microns) were utilized to collect the labeled plankton and bacteria in both the culture and primary productivity measurements. Determination of sample activity was made with a thin window gas flow counter.

To establish more quantitatively the importance of nitrogen contribution by alders to Castle Lake's nitrogen balance the amount of inorganic nitrogen inflow and outflow was compared with the average inorganic nitrogen content of the lake (based on 61 measurements on 16 sampling dates between June 9 and Oct. 29 at 0, 5, 15, and 30 m). A morphometric map of the lake was constructed, using a modification of Olson's (1960) system, to compute the volumes of water in each horizontal zone represented in the vertical nitrogen series.

The flow rate of 22 surface springs along the eastern shore was measured by damming each spring so that the overflow could be collected and measured. The outflow via Castle Creek was measured by determining the velocity and volume of water passing through a small culvert during high discharge and by collecting all the outflow from the culvert in a bucket for a timed interval during the late summer periods of low discharge.

Results and Discussion

The mean nitrogen content of alder leaves collected in June and August and the leaves of other deciduous species collected at the same times is compared with that of the leaves shed by the same trees and shrubs in the fall (Table I). Although the total nitrogen content (as percentage dry weight) of the green leaves is higher than that found in the freshly shed dry leaves, the total nitrogen content of alder leaves is consistently higher (about 35%) than that of the leaves of the other species. Although it is probable that some nitrogen was lost before the dry leaves were collected, the nitrogen content of alder leaves after defoliation amounted to over 4 times that found in the leaves of the other species and compares favorably with that in such leguminous plants as alfalfa.

Table I. A comparison of the total Kjeldahl nitrogen and nitrate content on a dry weight basis of leaves collected from alders along the east shore of Castle Lake with those of the other deciduous plants found around the lake

	Alder Leaves			Other Deciduous Leaves		
	No. of samples	% Total N[3]	ppm NO_3^- N	No. of samples	% Total N	ppm NO_3^- N
Green leaves[1]....	11	3.52 ± .19	199 ± 17	9	2.30 ± .12	255 ± 29
Leaf Fall 1959...	2	2.31	400	1	0.52	400
Leaf Litter[2].....	2	3.10	115	—	—	—

[1] Green leaves were collected in June and August 1959 and 1960.

[2] Leaf fall of 1959 collected in June 1960.

[3] Although NH_4^+ values were obtained for the leaf fall they are omitted because they represent onset of decomposition and are included in the total Kjeldahl nitrogen extractions.

Because of the slower decomposition of leaf proteins in relation to the more soluble fractions, the percentage nitrogen remaining in the alder leaf material increased during their winter on the ground. For the same reason the inorganic nitrogen content declined in relation to the organic.

The effect of the decomposition of these nitrogen-rich leaves on the fertility of the lake shore is quite evident when the soil and sediment are examined (Table II). Soil collected beneath the alders is very significantly higher in organic and inorganic nitrogen than soil taken from beneath the other deciduous plants. The highest value of the 21 soil profiles collected (2.52% total nitro-

TABLE II. Mean values for organic and inorganic nitrogen analysis of soil, sediment, and spring water from Castle Lake. Soil and sediment values are on the basis of dry weight of the samples

	EAST SIDE (beneath alders)					WEST SIDE				
	No. of samples	% Total N	ppm NO_3^- N	ppm NO_2^- N	ppm NH_4^+ N	No. of samples	% Total N	ppm NO_3^- N	ppm NO_2^- N	ppm NH_4^+ N
Soil Profiles										
0-5 cm.....	5	2.39± .07	6.6	.08	146	6	0.46± .04	2.2	.00	14
						2[1]	1.74± .05			
0-10 cm....	4	2.38± .10	1.5	.13	85	4	0.75± .12	0.7	.00	5
Lake sediment										
0-5 cm.....	1	0.60	0.8	.00	34	1	0.52	1.7	.00	22
Spring Water[2,3]	5	—	.337	.0005	.052	5	—	.032	.0000	.025

[1] Samples from beneath one of the few alders along the west shore.

[2] Samples taken from June through October.

[3] Lake Nitrogen was sampled on 16 dates from June to October at depths of 0, 5, 15, and 30 m. The average values for the summer at these depths for NO_3^- N, NO_2^- N, and NH_4^+ N were: 0.0569, 0.0000+, and .0527 g/m^3 respectively.

gen) was found on the east side in the upper 5 cm of humus beneath the alder canopy. The one high value of the west shore profiles was from directly beneath one of the isolated alders at the shore line. The only other recognized nitrogen-fixing plants noted on the watershed were the legume, *Lupinus,* and the myxophycean, *Nostoc,* which were not abundant.

The nitrate and ammonia content of spring water draining into the lake from both sides provides further evidence of the nitrogen contribution of the alders on the east shore (Table II). Analyses of the springs along the west shore from June to October showed no detectable nitrite. Very low levels were detected in July, August, and October in the East Spring water. The ammonia content of the springs draining the alders averaged twice that of the west shore springs with a maximum difference noted in August. The nitrate concentration of the alder springs averaged over 10 times the average of the west shore springs for the same sampling periods and reached a maximum value of over 1 ppm in August 1959.

The significance of the fertilizing effect of this spring water inflow was evaluated in 3 ways. First, spring water collected from the alder and non-alder side was assayed by addition of 1% by volume to cultures of Castle Lake water containing the lake's natural phytoplankton population (Figure 2). The greater nutrient value of the east shore spring water as compared with the west is evident from this experiment. Since the conductivity and cation composition of the east spring was slightly higher than the west spring on one occasion and slightly lower on another, it was desirable to bioassay water from the east shore before and after it had passed over the decaying alder leaves to separate the nutritional contribution of the leaves from that of the spring water itself. This was accomplished in the laboratory in May as soon as melting snow exposed the springs. The addition of spring water collected from a shallow cut several meters above the water's edge increased the rate of photosynthesis in lake water collected the same day by 5.4% in 4 hours. Water which was collected from the same spring after having flowed over an accumulation of alder leaves increased photosynthesis over the same control by 12.5%. During a warmer period with faster decomposition of the leaf mat, it is probable that the contribution would be greater.

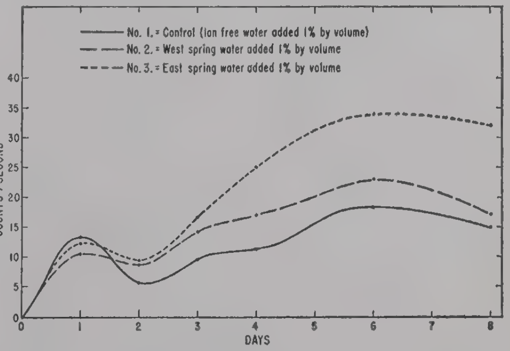

FIG. 2. Biossay with C^{14} of the relative nutrient contribution of spring water from the east and west sides of Castle Lake to culture growth of the lake's natural phytoplankton population in July 1959.

The 2nd means of assessing the fertilizing effect of the alder trees was a simultaneous measurement of primary productivity on both sides of the lake (station locations are indicated in Fig. 1 by circles). The higher rate of photosynthesis at the same depths on the east side of the lake during a four hour period at mid-day when neither side was shaded is quite evident (Figure 3). A comparison of the areas contained by the east and west primary productivity curves indicates a photosynthetic carbon fixation rate 17.1% greater near

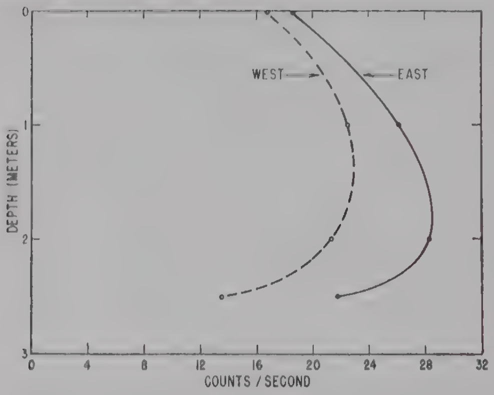

FIG. 3. Relative photosynthesis as measured by C^{14} uptake in Castle Lake on the east and west sides during a four hour *in situ* experiment on 27 August 1959.

TABLE III. Castle Lake measured and estimated nitrogen budget for 120 days from midJune to midOctober 1960

	Volume[1] (m^3)	Concentration (g/m^3)	Total (kg)[2]	Total (kg/summer)	Total as % of the amount in lake
In the lake	1,910,106	0.0886	169.27	—	—
Outflow	806	0.0638	0.0513	6.156	3.6
Surface inflow from East Springs	561	0.389	0.218	26.16	15.5
Estimated inflow[3]					
100%	1,386	0.389	0.539	64.7	38
80%	1,386	0.311	0.431	51.7	31
60%	1,386	0.233	0.323	38.8	23
40%	1,386	0.156	0.216	25.9	15

[1] Inflow and outflow values are in m^3/day.

[2] Inflow and outflow values are in kg/day.

[3] The estimated nitrogen inflow is based upon evaporation loss (a minimal average value of 3.81 mm/day) from the lake surface plus the average measured daily outflow. Because the subterranean drainage of the east shore probably contains less nitrogen than the surface spring water and a small portion enters from the three west springs, values are given for different percentages of the measured nitrogen inflow (0.389 g/m^3/day).

the east shore. A better development of the higher aquatic plant *Isoetes* along this shore is also suggestive of higher fertility.

The 3rd approach, for a more quantitative evaluation of the alder contribution to the lake as a whole, was measurement of the lake's inorganic nitrogen budget from June through October 1960 as described in "methods." The average inorganic nitrogen content of the lake during this period was 169.27 kg in just over $1.91 \times 10^6 m^3$ (Table III). The surface nitrogen inflow from the east springs amounted to 26.16 kg (15.5% of the lake's average total inorganic nitrogen) during the summer. The measured inflow is certainly a conservative estimate, as much of the nitrogen-rich spring seepage enters the lake below the surface of the ground and could not be directly measured. This is indicated by the greater stream discharge volume in comparison to the measured inflow. Evaporation rate from the lake surface was estimated at 3.81 mm/day with a class A U. S. Weather Bureau evaporation pan for 24 hours from 8 to 9 September 1960. Relative humidity (measured with a sling psychometer) varied from 22% to 73% and the day was cloudy with little wind. Solar radiation was well below average and air temperature ranged from 13 to 24°C.

A more realistic estimate of the inflow is based on outflow volume and the minimal evaporation value obtained in September (Table III). If the inorganic nitrogen content of the drainage water was 80% of that carried in with the surface spring water the lake is actually receiving twice the amount of nitrogen measured. The measured accumulation in the lake (inflow nitrogen minus outflow) would amount to 20 kg for the 120 day period from mid June to mid October. The trout yields from 1956-1959 have averaged 6.05 kg/acre year or 290.4 kg/year for the lake (Wales and Borgeson 1961). On the basis of a 20% protein content the annual nitrogen removal as fish would be 9.3 kg. The remainder can be assumed to recycle or be lost through insect emergence, sedimentation, organic nitrogen outflow, and possibly denitrification.

No attempt was made to determine if there were nitrogen fixation in the lake; however, nitrogen-fixing blue green algae were not observed in the plankton. If microorganisms were fixing nitrogen in Castle Lake at as high a rate (0.068 mg/m^3/day) as that reported for water from the Pymatuning Reservoir (Dugdale *et al.* 1959), 0.068 kg N/day would be added from the Castle photic zone. This would be 31.2% of the measured nitrogen inflow from the east shore springs.

The high efficiency of alders in nitrogen fixation is evidenced by a greater fixation by their nodule tissue per unit dry weight than that of legumes grown under the same conditions (Ferguson and Bond 1953). Lawrence (1958) has found that young alder thickets 5 years of age add 140 pounds of nitrogen per acre to the soil each autumn and greatly stimulate the growth of associated cottonwood trees. The stimulating effect of the alder leaves on the primary productivity of Castle Lake is apparent from both the culture and the *in situ* measurements of primary productivity. The nitrogen content of leaves, soil, sediment, and spring water on the east side of the lake indicate that the alders are a significant source of nitrogen. Their importance to the overall metabolism of Castle Lake, and in all probability to any lake or stream whose drainage area supports appreciable numbers of nitrogen fixing terrestrial plants, is evidenced by both the measured and estimated inorganic nitrogen contribution to the lake. Preliminary pollen extractions from cores indicate that the alders have been present on the lake shore during the accumulation of at least the first 36 cm of sediment.

The rainfall at Castle Lake, although very light during the summer months, contained almost as much NH_4^+ in September (0.4 ppm) as the spring water analyzed in August. The NO_3^- content of the spring water (1.0^+ ppm), however, was much higher at this time. The major portion of the nitrogen from the springs along the alder side of the lake is in the form of NO_3^- or perhaps organic forms which may actually be preferred by some phytoplankton (Krauss 1958). The NO_3^- levels in the lake remained well above the NH_4^+ (if the hypolimnion (30 m) values are excluded) until late September. If the molybdenum deficiency on Castle Lake (Goldman 1960b) is limiting the action of nitrate reductase, added molybdenum might provide for a more efficient nitrate utilization by the phytoplankton. Molybdenum has been demonstrated to be essential for the growth of some algae when NO_3^- is the sole nitrogen source (Arnon *et al.* 1955).

The loss of nutrients by plant leaves to rain or dew has been recognized for many years (LeClerc and Breazeale 1909), and the fertilizing influence of drip from the forest canopy when light is not limiting has been measured in terms of moss production by Tamm (1950). Although quite variable, average total rainfall for July, August, and September at Mt. Shasta near Castle Lake is only 1.08 inches (2.74 cm) (U. S. Weather Bureau 1959). It therefore seems unlikely that very much is added to the contribution of decaying alder leaves by leaf drip except perhaps in June or late September. A more important consideration is probably the alder leaves which are blown into the lake.

The reservoir of nitrogen in the form of decaying alder leaves along the east shore of Castle Lake is of special importance since the springs provide the lake with a continuous recharge of this essential element and perhaps other growth factors during the major portion of the year. In respect to other growth factors it is of interest that the alder and other deciduous leaves contained detectable quantities of molybdenum. The high NO_3^- content of the east springs suggests the continuous activity of nitrifying bacteria in the humus layer which oxidize the NH_4^+ to NO_2^- and then to NO_3^- following the decomposition of leaves by saprophytic bacteria. Only in late summer when the water table fell below the leaf mat did the nitrogen content of the water decline.

Biological agents in the lake may remove additional NO_3^- and NH_4^+ with increase in primary productivity but without much environmental change in these nitrogen levels. It is therefore of considerable importance to consider the rate of change within the system rather than to rely on measures of relative concentration. The quantity and quality of replenished nutrients are important in establishing the level of primary productivity in Castle Lake and may be expected to influence the rate of growth at successive trophic levels.

SUMMARY

The abundance of the mountain alder (*Alnus tenuifolia* Nutt.) along the east shore of Castle Lake provided an opportunity to evaluate the influence of this nitrogen-fixing terrestrial plant on the primary productivity of the lake.

Total nitrogen content of green alder leaves was appreciably higher than that of other deciduous species. Analyses indicated that the leaf fall from the alders contained over 4 times as much nitrogen as the defoliation from other species.

Soil analyses clearly indicated the accumulation of nitrogen on the alder side of Castle Lake as well as in the lake bottom sediment. Springs draining the east shore also reflected the higher nitrogen levels on the alder side. The measured inflow of inorganic nitrogen amounted to 15.5% of the lake's average content during the June to October period. Estimates based on evaporation loss and measured outflow of the lake considerably increase this value. A total inorganic nitrogen budget for the lake was estimated.

The greater fertilizing influence of the spring water from the east shore over that collected from the west was demonstrated by bioassay utilizing C^{14}, the natural lake phytoplankton, and filtered spring water as a nutrient additive. In a 2nd experiment the stimulating effect of the east shore spring water on culture growth was doubled after passage through the alder humus.

Simultaneous *in situ* measurement with C^{14} of photosynthesis in Castle Lake gave further evidence of a significant contribution by alders to the primary productivity of the lake.

ACKNOWLEDGMENTS

This study was supported by National Science Foundation grant 8901 and by Dingell-Johnson Project California F-8-R supported by Federal Aid to Fish Restoration funds. Dr. A. J. Calhoun, California Department of Fish and Game, was instrumental in establishing the latter support. J. H. Wales, who directed the trout studies at Castle Lake from 1938 to 1958, encouraged the author to use Castle Lake for this investigation. Other Department of Fish and Game personnel, G. W. McCammon, D. P. Borgeson, H. R. Cochran, R. C. Richards, and E. D. Bailey provided invaluable assistance in the field work and logistics of the study. Faculty and staff of the University of California at Davis who provided valuable assistance were: D. T. Mason of the Zoology Dept.; Miss June McCaskill, Department of Botany Herbarium, who identified the plant material; Dr. F. E. Broadbent and J. Quick who made the nitrogen analyses of soil and plant material. Flame spectrophotometric analyses were made by Mrs. Ann Quek.

REFERENCES

Allen, E. K., and O. N. Allen. 1958. Biological aspects of symbiotic nitrogen fixation. In: Encyclopedia of plant physiology. Vol. 8. W. Ruhland Ed. Berlin, Springer-Verlag.

American Public Health Association et al. 1955. Standard methods for the examination of water, sewage, and industrial wastes. 10th Ed. New York, American Public Health Association.

Arnon, D. I., P. S. Ichioka, G. Wessel, A. Fujiwara, and J. T. Woolley. 1955. Molybdenum in relation to nitrogen metabolism. I. Assimilation of nitrate nitrogen by *Scenedesmus.* Physiol. Plant. **8**: 538-551.

Bond, G., W. W. Fletcher, and T. P. Ferguson. 1954. The development and function of the root nodules of *Alnus, Myrica,* and *Hippophae.* Plant Soil **5**: 309-323.

Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecol. **43**: 427-448.

Dugdale, R., V. Dugdale, J. Neess, and J. Goering. 1959. Nitrogen fixation in lakes. Science **130**: 859-860.

Ferguson, T. P., and G. Bond. 1953. Observations on the formation and function of the root nodules of *Alnus glutinosa* (L.) Gaertn. Annals Bot., N.S. **17**: 175-188.

Forbes, S. A. 1887. The lake as a microcosm. Reprinted in 1925 in Bull. Ill. Nat. Hist. Surv. **15**: 537-550.

Goldman, C. R. 1960a. Primary productivity and limiting factors in three lakes of the Alaska Peninsula. Ecol. Monogr. **30**: 207-230.

———. 1960b. Molybdenum as a factor limiting primary productivity in Castle Lake, California. Science **132**: 1016-1017.

Hiltner, L. 1896. Über die Bedeutung der Wurzelknöllchen von *Alnus glutinosa* für die Stickstoffernährung dieser Pflanze. Landw. Versuchsstat. **46**: 153-161.

Johns, C. A. 1849. Forest trees of Britain. London, Samuel Bentley and Co. Vol. 2.

Krauss, R. W. 1958. Physiology of the fresh-water algae. Ann. Rev. Plant Physiol. **9**: 207-244.

Lawrence, D. B. 1958. Glaciers and vegetation in southeastern Alaska. Amer. Sci. **46**: 89-122.

LeClerc, J. A., and J. F. Breazealle. 1909. Plant food removed from growing plants by rain or dew. U.S. Dept. Agric. Yearbook, 1908: 389-402.

Olson, F. C. W. 1960. A system of morphometry. Int. Hydrogr. Rev. **37**: 147-155.

Reimers, H. 1954. Untersuchungen über die Wirkung des Laubfalles auf die productionsbiologischen Faktoren in einem fischereilich genutzten Gewässer. Ph.D. Dissertation, Univ. of Hamburg.

Rider, B. F. and M. G. Mellon. 1946. Colorimetric determination of nitrites. Ind. Eng. Chem., Anal. Ed. **18**: 96-99.

Steemann Nielsen, E. 1952. The use of radioactive carbon (C^{14}) for measuring organic production in the sea. J. Cons. Int. Explor. Mer **18**: 117-140.

Tamm, C. O. 1950. Growth and plant nutrient concentration in *Hylocomium proliferum* (L.) Lindb. in relation to tree canopy. Oikos **2**: 60-64.

Thienemann, A. 1950. Wesen und Bedeutung der Limnologie. Oikos **2**: 149-161.

U. S. Department of Commerce Weather Bureau. 1959. Local climatological data. Mount Shasta, California.

Virtanen, A. I., and S. Saastamoinen. 1933. Über die Stickstoffbindung bei Erlen (*Alnus*). Acta Chem. Fennica **6**: 57-58.

———, ———. 1936. Untersuchungen über die Stickstoffbindung bei der Erle. Biochem. Z. **284**: 72-85.

———, **T. Moisio, R. M. Allison, and R. H. Burris.** 1955. Fixation of nitrogen by excised nodules of the alder. Acta Chem. Scand. **9**: 184-186.

Wales, J. H. 1946. Castle Lake trout investigation. First phase: interrelationships of four species. Calif. Fish and Game **32**: 109-143.

———. 1947. Castle Lake investigations: 1947 catch and chemical removal of all fish. Calif. Fish and Game **33**: 267-286.

———, **and E. R. German.** 1956. Castle Lake investigations. Second phase: eastern brook trout. Calif. Fish and Game **42**: 93-108.

———, **and D. P. Borgeson.** 1961. Castle Lake investigation. Third phase: rainbow trout. Calif. Fish and Game (in press).

SOME DYNAMICS OF SPATIAL DISTRIBUTION WITHIN SEMI-NATURAL POPULATIONS OF PRAIRIE DEERMICE[1]

C. RICHARD TERMAN
Penrose Research Laboratory, Zoological Society of Philadelphia, Philadelphia, Pennsylvania

INTRODUCTION

The distribution of an animal species in space may be geographical or local in scope. Geographical distribution of a species is measured in terms of the range of occurrence of its naturally existing populations. This treatment of distribution is essentially historical and has great descriptive and comparative value. A species, however, is a "dynamic system" (Blair 1956), whose basic components are local populations existing in equilibrium with the ever-changing environment. Therefore, the study of factors influencing spatial distribution within local populations offers a dynamic approach to many problems associated with the spread of a species over its broad geographical range.

---

[1] This investigation was supported by the R. B. Jackson Laboratory, Bar Harbor, Maine, through Grant C. R. T. 5013 while the author was a Pre-doctoral Research Fellow at the Laboratory. Most of the data presented in this report are included in a dissertation submitted to the Zoology Department, Michigan State University, in partial fulfillment of the requirement for the Ph.D. degree.

Spatial distribution within populations of small mammals living under semi-natural conditions is related in a complex way to the influence of the physical as well as of the biotic environment.

The importance of characteristics of the habitat in determining spatial distribution has been indicated by numerous studies. Brand (1955) studying the white-footed mouse (*Peromyscus leucopus noveboracensis*) has shown a direct seasonal relationship between the distribution of the population and tree density, degree of slope, and density of fallen trees. The significant factors of the habitat in this relationship probably were occurrence of food and potential nest sites. Orgain and Schein (1953) effected a decrease in the numbers of rats in city blocks for a short period of time by removing some of the harborage sites. Davis (1958) changed the spatial distribution within laboratory populations of house mice through the introduction of baffles and additional nest sites into the study area. The relationship of distribution and abundance of natural populations of *Peromyscus* to habitat differences was shown by Provost (1940) and Blair (1951).

Location of food may be a factor influencing spatial distribution under semi-natural conditions in populations of rats (*Rattus norvegicus*) (Calhoun 1949, 1950, 1952) and house mice (Strecker 1954). Similar results were obtained under natural conditions with rats (Orgain and Schein 1953) and house mice (Brown 1953).

That population size and competition are important in determining spatial distribution is evident from Calhoun's (1950) study of a freely growing rat population in a quarter-acre enclosure constructed to provide a gradient of accessibility to the food. Rats born near the source of food maintained their home areas more effectively and forced animals living in submarginal areas to remain there.

Stability of spatial distribution related to the number of animals in an area has been shown by experiments in which part of the population was removed. Stickle (1946) and Blair (1940) with *Peromyscus,* Orgain and Schein (1953) with rats, and Calhoun and Webb (1953) with several species of small mammals, demonstrated the tendencies of animals living in surrounding areas to move into vacated areas following removal of the residents. Animals released into areas already populated by members of the same species either rapidly dispersed (Blair 1940, Calhoun 1948) or disrupted the population and brought about a temporary decrease in population numbers (Davis and Christian 1956).

The nature of social factors influencing spatial distribution in local populations of small mammals has not been clearly demonstrated. Territoriality, defined as defense of an area (Noble 1939), has been suggested to explain spatial patterns of distribution in small mammals. While territorial behavior is of widespread occurrence in birds (Howard 1920, Nice 1941), such behavior in small mammals is a matter of controversy (Blair 1953, Burt 1940, 1943, 1949, Crowcroft 1955, Scott 1944). If territoriality does exist as a characteristic mechanism maintaining spatial distribution relative to the physical environment and the biology of most species, what social factors are important in the establishment and maintenance of such behavior? If teritoriality is not characteristic of all species, what social mechanisms effectively regulate spatial patterns of distribution in non-territorial species? Do differences in the social behavior of the individual animals of the population affect spatial distribution?

This study was designed to combine laboratory and field techniques in order to examine the significance of social factors in the spatial distribution of prairie deermice within local populations.

The objectives of this investigation were:

1. To study the influence of social manipulation of deermice populations in the laboratory upon the subsequent spatial distribution of these mice in a semi-natural environment.
2. To examine behavior patterns affecting spatial distribution in free-ranging, semi-natural populations.
3. To measure the individual awareness of and preference for the home area as well as the stability of such an area.

This paper is primarily concerned with the results obtained relating to objective 2.

MATERIALS

Experimental animals

The prairie deermouse (*Peromyscus maniculatus bairdii* Hay and Kennicott) inhabits prairies, open fields, beaches, and dense grass along fence rows in the midwestern United States. It was selected as the experimental animal because a grassland form was considered best suited to the study contemplated and quantities were available from a laboratory colony. No native grassland species of *Peromyscus* occur in Maine where this study was conducted. An attempt was made to correct for any ecological imbalance between the maritime environment and the adaptability of this subspecies by providing food, nest sites, and nesting material in excess of need. The biology of the experimental mice in terms of reproduction, weight, general body condition, and survival indicated that this attempt was successful, at least for the short periods under study.

Although natural populations of prairie deermice have been extensively studied (Blair 1940, Dice 1932, Howard 1949), the factors involved in the spatial distribution of local populations are unknown. Burt (1949) suggested that territoriality is a part of the behavior pattern of many species of animals and results in population dispersal. On the basis of live trapping and nest box studies of wild populations, Blair (1940, 1953) and Howard (1949) concluded that *P. m. bairdii* does not show intra-specific antagonistic behavior and thus is nonterritorial in the defined sense. Howard, however, postulated that prairie deermice exhibit some kind of natural negative response to crowding beyond a certain density within a limited area, but he was not able to describe, measure, or demonstrate the existence of any such negative force.

Laboratory facilities

The mice were born in the laboratory and most were born in a colony of 60 breeding pairs. All the animals were descendants of 12 original pairs whose offspring had been in the laboratory for approximately 15 generations.

The mice were kept in basement rooms in the Behavior Division of the Roscoe B. Jackson Memorial Laboratory. Lights were on in these rooms from approximately 7:30 AM to 4:30 PM each day. The mice were housed in 2-compartment wooden boxes, and were provided with Purina laboratory pellets and water in excess of utilization. The floor of each box was covered with a thin layer of wood shavings, and the mice were placed in other, clean boxes every two weeks.

Experimental field

The experimental area was a 0.9 acre field located at the Hamilton Station of the R. B. Jackson Laboratory, Bar Harbor, Maine. The field was 250 feet long and 165 feet wide with the length having a compass bearing of NE-SW. A gradual slope in the longitudinal direction from SW to NE caused runoff of water toward the NE end during heavy rains.

The vegetation of the field was studied by recording species composition and distribution and the distribution of plant mass (Terman 1959). The vegetation was predominantly herbaceous, although forbs were found in quantity in parts of the field. Plot B contained a significantly greater mass of vegetation than Plot A ($.05 > P > .01$).

Enclosure

Figure 1 is a map of the experimental field. The area was divided into two 0.44 acre plots, each 240 by 80 feet, and surrounded by corrugated aluminum partially buried on edge in the ground (Figure 2). The rolls of aluminum measured 100 feet by 28 inches and were buried to a depth of 8 inches. Since the two plots were adjacent, a single piece of aluminum served as a common inside boundary. The entire area was surrounded by a 7-foot high wooden fence to which wire fencing was attached at the bottom and buried in the ground.

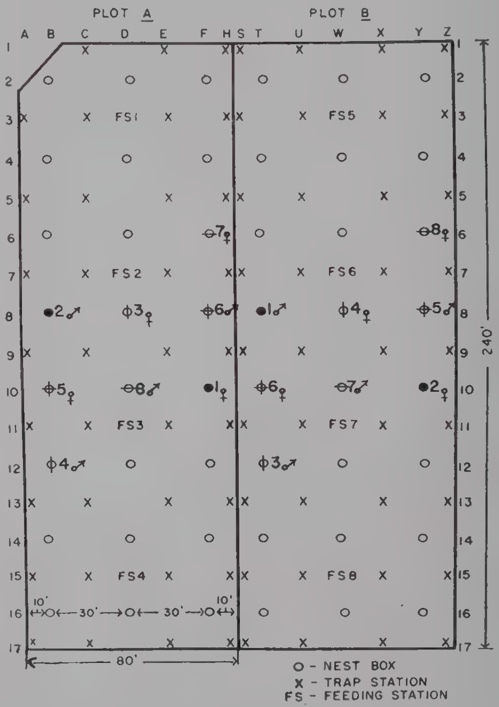

FIG. 1. Design of the experimental field and the pattern of introduction of the mice into the plots. Individuals of closely associated pairs were released into nest boxes characterized by identical symbols.

Nest boxes

Twenty-four subterranean boxes, represented by circles in Fig. 1, were placed in each plot along 3 files and 8 ranks. In Plot A these files were B, D, F, and in Plot B they were T. W. and Y. The even-numbered ranks indicated nest boxes in both plots. Each nest box was 30 feet from its nearest neighbor in the same file or rank. Nest boxes in

FIG. 2. North-east view of the experimental field along the partition between plots.

files B and F in Plot A, and T and Y in Plot B were 10 feet from the longitudinal aluminum fence nearest them. The end nest boxes in each plot were 15 feet from the end fence.

Each nest box (Figure 3) was built of ½ inch lumber and had the following outside dimensions: 6½″ wide × 5¾″ deep × 7″ high. The nest chamber was floored by a piece of hardware cloth and roofed with a ceiling of hardboard. An air space of 1″ for insulation was present between the ceiling of the nest chamber and inside surface of the lid of the nest box. A 6″ piece of white rubber laboratory hose provided a pliable entrance tunnel of 1″ inside diameter. Each nest box was saturated with paraffin and the hose entrance tunnel was heavily coated at the point of connection with the box. This method of preparing the boxes was effective in providing a waterproof nest site for the mice.

Each nest box was completely buried in the ground. The top was covered by a piece of heavy roofing material and a large piece of sod.

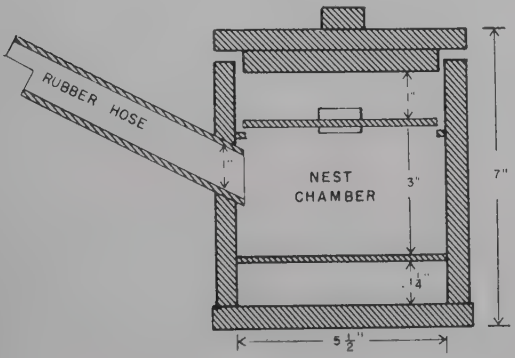

FIG. 3. Diagram of a nest box.

Box traps

There were 4 files of trap stations (X in Fig. 1) alternating with the files of nest boxes in each plot. Because of a variation in the eastern outside boundary of Plot A, there were only 35 trap stations in this plot, while Plot B contained 36. Two single catch, box-type live traps were placed at each trapping station within the area enclosed by the aluminum fence. At each marginal trap station one additional trap was located outside the aluminum fence and was left set continually. Thus, a total of 169 live traps were used in the experiments, of which 27 were located outside the enclosure.

Feeding stations

Food, provided in excess of utilization, was placed in a small hardware cloth hopper to prevent hoarding. One hopper was placed at each of 4 feeding stations (FS in Fig. 1) in each plot located at the intersections of files D and W with ranks 3, 7, 11, and 15. The feeding stations were continuously in the field and were distributed equidistant from the nearest nest boxes.

PROCEDURES

Laboratory procedures

The young mice remained with their parents in the laboratory until 3 weeks of age. They were then separated from their parents and randomly placed either in a group or in isolation. Litters were selected for social treatment by the criteria that birth must have occurred within a 9 day period centered around a day 70 days prior to the scheduled date of release into the experimental field, each litter must have contained at least one male and one female, and both parents must have survived until the date of weaning. Since this report is concerned with the population information obtained independently of the social treatments, a more thorough discussion of these treatments will not be made here.

During the treatment period, food (Purina laboratory pellets) and water were supplied in excess of use and the animals were moved to other, clean cages every 2 weeks. Both treatment populations were kept in their respective social situations until release into the field at 10 weeks of age. At this age the mice were physically and reproductively mature (Clark 1938, Dice and Bradley 1942).

Eight mice from each social treatment were released into different one-half acre plots of the field during each experimental period. Animals to be released were selected according to 2 specifications. First, no pregnant females were acceptable. Pregnancy was ascertained by inspection and palpation. Second, populations released in the field were composed of a male and a female from each of 4 litters.

Henceforth, in this discussion, those mice which were introduced into the field will be referred to as experimentals and those remaining in the laboratory in their original social treatments, as controls.

On the day preceding scheduled introduction into the field, both the experimentals and the controls of each social treatment were etherized, weighed, and numbered by toe clipping. In addition, all experimental mice were tagged with a colored celluloid disc attached to one ear by a numbered fingerling tag.

Field procedure

Introduction into the field

Prior to the introduction of each experimental population into the field, the nest boxes in each plot were cleaned. Clean cotton nesting material and 5 pellets of Purina laboratory mouse food were then placed in each box.

The experimental mice were released in the field at least one hour before sunset on the same day that the previous populations were removed. This was also true for the first experiment since preliminary populations preceded it. Release of populations raised in each social treatment alternated between plots A and B for successive experiments. The experimental populations were introduced into the plots as systematically as possible since preliminary work indicated that releasing the populations at the center of each plot resulted in high mortality. Thus, a pattern of introduction into nest boxes was followed for each plot and was repeated for the 8 experimental periods.

The experimental mice were assigned to nest boxes by using the most closely associated pairs as the basic unit for distribution (Fig. 1). The isolation treatment was represented by 4 sib-pairs, the individuals of each pair having been raised in separate compartments of the same mouse box. The most closely associated group-raised pairs were not sibs, as in the case of the isolates, but were mice that had lived together since weaning. Males and females of each closely associated pair were released into nest boxes separated from one another by a distance of 67.1 feet. In addition, the pattern of introduction of the animals of each population was such that the nearest neighbors of the same sex were separated by a distance of 42.4 feet, and those of the opposite sex by 30 feet. This procedure assured that:

(a) Naïve animals gained experience with one nest box.

(b) Original distribution patterns were constant for each experimental population no matter into which plot it was placed.

(c) Individuals of all closely associated pairs were initially equidistant from each other.

(d) All mice were equidistant from the nearest neighbor of the same sex.

(e) All mice were equidistant from the nearest neighbor of the opposite sex.

Period of population establishment

A period of 17 days after introduction was considered sufficient for the mice to establish themselves in the field in a relatively stable manner. The 17-day period was chosen arbitrarily after inspection of data collected in preliminary experiments.

During the "period of population establishment" daily inspections of all nest boxes in each plot were made and the location of each mouse recorded. No time schedule was followed for examining the nest boxes in each plot and, since all mice wore celluloid discs of a different color on one ear, it was not necessary to handle them for identification.

Two periods of live trapping were conducted while each population was in the enclosure. Both trapping periods were of 4 nights' duration and, on each night, traps remained set until 2 hours after sunset. At this time the mice caught in the traps were recorded and released. The first trapping period began on the 2nd night the mice were in the field and continued through the 5th night after introduction. The second trapping period was conducted on the 14th, 15th, 16th, and 17th nights of each period of population establishment.

Homing

Seventeen days after introduction into the plots, all mice were removed and kept in isolation in the laboratory for 36 hours. Each mouse was then returned to its home plot and released at a point distant to its previously established home area. The location of each mouse for the next 3 days was recorded. This procedure constituted the homing phase of these experiments, the data for which will be discussed in a subsequent paper.

Population removal

On the 3rd morning of the homing phase of each experiment, the mice were taken from the nest boxes, killed with chloroform, weighed, and the adrenal glands removed and weighed. The nest boxes were then cleaned and readied for the introduction of the next experimental population.

General procedures

Observations

The nocturnal activities of the mice were observed with a flashlight or with the 7 floodlights in the field. Most observations were made immediately after release of the mice from the traps at 2 hours after sunset or while alien mice were tethered either near the feeding stations or in the vicinity of nest boxes known to be occupied by resident mice. Alien mice were used to promote social interaction and were removed from the field at the close of each observation period. The aliens wore collars made of small fishing tackle snaps. A fine, 6-inch wire leader was attached to a swivel on the collar and then to a stake in the ground. Since there were swivels at both ends of the leader, each mouse was free to move within a circular area of radius equal to the length of the leader. This confinement did not appear to impede the mice from moving about and manipulating their bodies. The collars apparently were not detrimental to the mice since they were worn in the laboratory for several months with no ill effects.

Predation control

Predation was not an important factor in this research, for only 7 out of 128 experimental animals disappeared during the periods of population establishment. Nevertheless, a steel trap was continuously set near each of 5 feeding stations to insure against predatory mammals.

RESULTS

The data presented here suggest the existence of phenomena that may be specific to populations of prairie deermice, to mice of the species *Peromyscus maniculatus,* or that have general significance with regard to small mammals. Accordingly, only those measurements will be presented which reveal factors operating independently of the 2 laboratory social treatments.

Descriptive measurements

A prerequisite to meaningful analysis and interpretation of the data is an understanding of the adaptation of the populations to the experimental situation. The following descriptive measurements were taken as a means of gaining this understanding:

Number of mice

There were 8 experimental periods, each of 3 weeks duration, between June 6 and November 21, 1958. A population of 4 males and 4 females, raised either in isolation or in groups, was in each of the 2 plots of the field during every experimental period. Thus, the total number of mice released into the plots was 128, of which 64 were reared in each of the 2 social situations.

Use of nest boxes

A total of 1884 occurrences of mice in nest boxes was recorded during the periods of population establishment. The period of population establishment for 5 of the 8 populations of each social treatment was 16 days instead of the originally planned 17. This occurred because a few mice avoided capture and could not be removed from the plots on the day scheduled. Therefore, the next succeeding population was introduced into the plot one day late. Further, of the 128 mice released into the plots, 4 died and 7 disappeared during the period of establishment. Adjusting for these deviations in the design, a total of 2008 recordings of mice in nest boxes was possible during the experiments. Thus, the mice were found in nest boxes 93.3% of the times possible.

A tabulation was made of the mean number of different nest boxes occupied per mouse during the period of population establishment and during the last 10 days prior to removal from the field for the homing test. During the total period of population establishment, the isolation-raised females and males were found in an average of 6.0 and 6.4 nest boxes respectively, while the group-raised females and males were found in 5.7 and 6.3 nest boxes each. In the last 10 days of each period of establishment, isolation raised females were found in an average of 4.3 nest boxes while males were in 4.4. Group raised females were in 4.2 boxes and males were in 4.3 during the same period of time. These data indicate no significant differences between sexes or social treatments in the average number of nest boxes occupied.

The fact that so few (mean of 6) of the 24 nest boxes in each field were occupied by each mouse may be indicative of a mutually realized division of the area and nest boxes among the several individuals of each population.

Moves between nest boxes

A daily tabulation was made of the average number of moves made per mouse to nest boxes not occupied on the previous day and to nest boxes in which the mouse in question had never previously been recorded. The first measure shows the rate of changing nest boxes on successive nights. It incorporates the second which inversely measures localization of the individuals.

The results of these measurements are shown in Figure 4 and indicate that:

(a) After a short period (1-3 days) of sedentary behavior subsequent to release in the field, a rapidly increasing proportion of the mice moved to different nest boxes each day until 7 or 8 of the period of population establishment.

(b) After day 7 or 8, the proportion of animals moving to different nest boxes became relatively constant, whereas the proportion moving to previously unvisited nest boxes became smaller with the passage of time. This downward trend of the curve measuring movements to strange nest boxes was not due to a decreasing availability of such nest boxes since an average of only 6 nest boxes per mouse was occupied in the total period of population establishment.

(c) There was a highly significant difference, as indicated by the t test, between the average daily number of moves to strange nest boxes and moves to boxes not occupied the previous day ($P < .001$). Thus, the mice continued to move to other nest boxes at a relatively steady rate, but an increasingly higher percentage of their movements were to a few previously visited boxes.

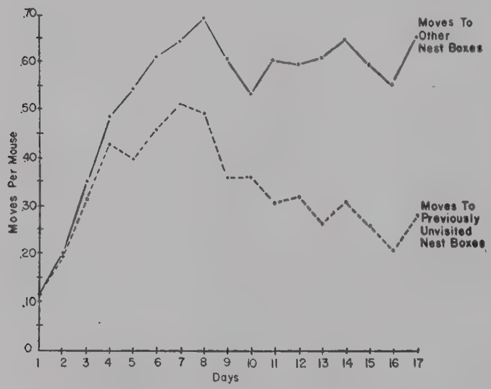

FIG. 4. Proportion of mice moving to other nest boxes and to previously unvisited nest boxes on successive days during the period of population establishment.

A further indication of the localization behavior of the mice following day 7 or 8 may be had by examining Figure 5. Here, the records of mice occurring in the same nest box as on the previous day were combined with those indicating movements to previously occupied nest boxes. The average daily proportions of mice exhibiting this localization behavior are plotted in Fig. 5 as are the mean daily proportions of mice which moved to previously unvisited nest boxes. Here, as in Fig. 4, the short period of sedentary behavior following introduction to the field may be seen. Further, after day 7, an increasingly higher proportion of mice either did not move or moved to previously occupied nest boxes. From day 8 through 17, there was a highly significant difference ($P < .01$) between the number of mice which were recorded in previously unvisited nest boxes and the number which localized. This was true in spite of the fact that the proportion of movements continued at a high level (Fig. 4).

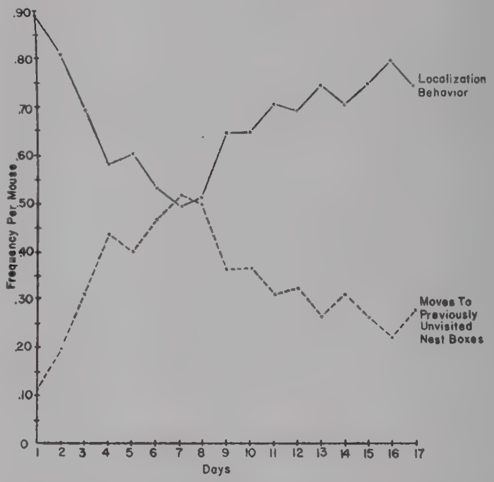

FIG. 5. Proportion of mice moving to previously unvisited nest boxes or exhibiting localization behavior on successive days during the period of population establishment.

Figure 6 compares movements to previously visited nest boxes and those to unvisited boxes on the basis of the number of moves recorded. It was not until 11 days after introduction into the plots that half the moves made were to each type of nest

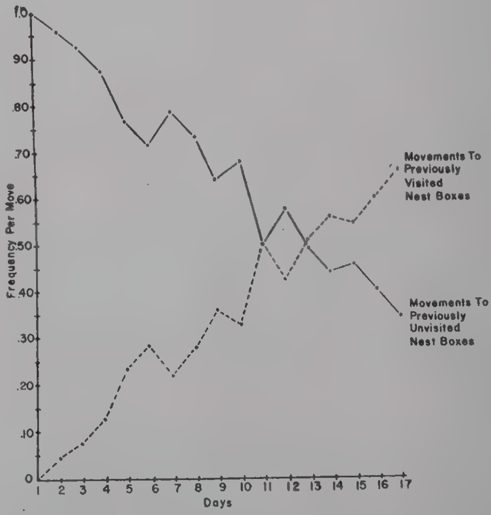

FIG. 6. Proportion of movements made to previously unvisited and to previously visited nest boxes on successive days during the period of population establishment.

box. From day 11 on, proportionally fewer movements were to unvisited boxes than were to previously visited boxes. This was true in spite of the fact that each mouse was recorded in an average of only one-quarter of the nest boxes in each plot. A comparison by the t test of the proportion of movements to visited or unvisited nest boxes subsequent to day 11 showed that a higher proportion of moves were to previously visited nest boxes. This difference, however, was not significant at the 5% level ($.2 > P > .1$).

Social relationships

Gregarious behavior

Table I indicates the total number of times mice were found in nest boxes alone, in pairs, or in groups of 3 subsequent to release in the field. It may be seen that the mice were most often found alone and rarely combined in other than bisexual pairs.

TABLE I. Occurrence of mice in nest boxes alone, in pairs, and in groups of three

	Isolation Raised	Group Raised
Mice Alone		
Males	379	351
Females	358	353
Pairs		
Male and female	84	103
Female and female	0	3
Male and male	4	2
Groups of three		
One male and two females	0	6
Two males and one female	3	5

It is of further interest to note that males never were recorded together before the last experiment (October 31 to November 21). Isolation raised females never occurred together. Among group raised females, however, 2 individuals in each of 3 populations were found together 3, 1, and 5 times respectively. It is evident that unisexual combinations were extremely rare, and that lower temperatures or other changes in the physical or biotic environment may have been responsible for the change in behavior during the last experiment.

Pair combinations

Chi-square tests of the observed frequencies of bisexual or unisexual pairs indicate that all combinations occurred in significantly ($P < .001$) different frequencies than expected by chance. Bisexual pairs occurred significantly more often and unisexual pairs significantly less often than expected.

In addition to recording the frequencies of occurrence of bisexual pairs, the individuals composing each pair and the duration (number of daily records) of each association were noted. Because of the aberrant grouping behavior which took place in the last experiment, data from that experiment are not included in this analysis. Only records of mice present in the plots on the 9th day after introduction are included. Fifty-five females and 52 males met this criterion. Of these, 42 females and 36 males were recorded in a bisexual pair at least once. There was no significant difference between sexes as to the proportion of each which combined in a bisexual pair.

Comparisons between sexes were made using only data obtained from animals that were found in a bisexual pair at least once. When data from like sexes from both social treatments were combined, males were found in a significantly larger number of different bisexual pairs than were females ($.05 > P > .02$).

Comparisons of the duration of bisexual pairs were made on the basis of animals combining at least once. When data for animals of the same sex were combined and compared by the t test, males were found to have been in bisexual pairs a significantly greater number of days than were females ($.02 > P > .01$).

The mean number of daily records in which each mouse was found with each mouse of the opposite sex was calculated. This calculation also was concerned only with mice which combined in bisexual pairs at least once. The data for each sex were compared by the t test and failed to show significant differences between the sexes as to the average number of days each animal occurred with each mouse of the opposite sex.

Establishment and termination of bisexual pairs

Mice were not recorded as bisexual pairs unless they were found together in a nest box at the time of the daily inspection. These data, therefore, offer a means by which sex differences in originating bisexual pairs may be inferred.

On the first day of each period of association, the location of the mice was recorded. Occurrence of each pair in a nest box occupied the previous day by the male or by the female was noted. Mice that moved into nest boxes occupied the previous

TABLE II. Originator and terminator of bisexual pairs

	Male	Female
Animal forming pair	31	30
Animal leaving first	30	19

day by the animal of the opposite sex were regarded as originating the bisexual pair. These data are tabulated in Table II.

Table II also contains a tabulation of the first animal leaving the bisexual pair. The totals of animals forming and leaving pairs are not the same because some mice were still in pairs when the experiments ended. Other pairs were enlarged to groups of 3. No significant differences were found between sexes as to which animal originated or terminated the bisexual pair.

Successive occupancy of nest boxes

As a further means of evaluating the individual responsibility for originating bisexual pairs, a tabulation (Table III) was made of the replacement of one mouse by another in a nest box on successive days. The sex of the mouse moving into the nest box and that of the mouse that had been in the nest box the preceding day was recorded. Records were made only when the animal moving out had not been living on the previous day with the one that replaced it.

TABLE III. Sex and frequency of mice occupying nest boxes on successive days

Succeed:	Male	Female
Male	9	27
Female	54	10

The frequencies with which each sex succeeded the opposite sex or the same sex were significantly different ($P < .001$). Animals of one sex were succeeded in nest boxes by mice of the opposite sex significantly more often than by mice of the same sex. Further, mice of the opposite sex succeeded each other significantly more often than expected by chance while mice of the same sex succeeded each other significantly less often than expected ($P < .001$). A comparison of the frequencies with which animals of the opposite sex succeeded each other and those expected by chance indicated that females succeeded males a significantly greater number of times than expected, while males succeeded females significantly less than expected. There was no significant difference between males and females in the frequency with which they succeeded animals of the same sex.

A further insight may be had by comparing the data measuring the originator of bisexual pairs (Table II) with the succession data discussed above. If the succession data are grouped assuming a tendency to leave or avoid combinations, the summation shown in Table IV may be made.

TABLE IV. Sex and frequency of mice avoiding or remaining in bisexual pairs

		Males	Females
Leave	Left nest boxes invaded by the opposite sex	54	27
Stay	Remained in nest boxes when the opposite sex came in	30	31

A significant difference was not shown (Chi-square) between males and females with regard to leaving or remaining in a nest box when a mouse of the opposite sex moved in. A P value of .06 indicates the tendency for males to leave more and remain less than females when a mouse of the opposite sex moved into the nest box. It should be remembered, however, that this analysis was made with the assumption that the mice left the nest boxes because an animal of the opposite sex moved into the box. The reverse may be true, that is, the immigrant animal may have moved into the box because the other animal had been there.

An additional evaluation of the data assuming a tendency toward combination may be made in the following way. In Table V the mice are recorded by sex with regard to (1) those succeeding an animal of the opposite sex in a nest box on successive days, (2) those which remained in a nest box when an animal of the opposite sex came in, (3) and those remaining in a nest box when the opposite sex left.

TABLE V. Sex and frequency of mice exhibiting "Pairing Tendency"

	Males	Females
Succeeded the opposite sex in nest boxes	27	54
Remained in nest box when the opposite sex came in	30	31
Remained in the nest box when the opposite sex left	19	30
Pairing tendency	76	115

A comparison of these data indicates that females exhibited a significantly greater tendency toward pairing than males ($P < .01$). Thus, males succeeded females less, remained in nest boxes less when females came in, and left the pair situation first in more instances than females. While these data are open to criticism with regard to their interpretation, they do suggest important considerations with regard to the dynamics of small mammal populations.

Observations

Nocturnal observations were made in the field to evaluate the type and extent of territorial behavior. Some observations were made of interactions between animals following their release from box traps in the field. Other observations were made at nest boxes known to be occupied by residents; alien mice were tethered outside of these and social interactions were observed when the residents left the boxes. A great deal of time had to be spent for each record obtained. While the number of observations are not large and the evaluation of the data are of necessity subjective, certain trends in the behavior of these animals were noted.

The data were grouped in the following manner and the frequency of each is given: Attacks (8): one mouse either attacked or directly charged the other mouse causing it to run away, submit, or assume a defensive posture (Agonistic behavior, Scott 1956). Avoidance (15): the animals saw each other and moved away from each other. Ignoring (2): the animals saw each other but no detectable repulsion or avoidance behavior took place.

Of the 5 attacks made upon aliens tethered outside residents' nest boxes, 2 were made by one female against 2 different aliens and 2 by one male against the same alien on successive nights. All attacks were of short duration and were terminated by the resident leaving the area. The attacks seemed designed to drive the aliens away but, since the aliens were tethered, this was impossible and resulted in the residents leaving instead. These relatively few data indicated that avoidance, or threat may be a method of apportioning the area among the animals of a population.

DISCUSSION

Factors affecting populations in the wild are difficult to ascertain experimentally because of lack of control of the experimental situation. Loss of animals due to dispersal (Blair 1940, Howard 1949, King and Eleftheriou 1957) and death from many causes make it difficult to control numbers while studying related variables.

This study was an attempt to combine the laboratory and field approach with a minimum of loss of their individual advantages (Schneirla 1950, Scott 1950). Thus, the biology of populations, both physical and social, may be studied under semi-natural conditions while maintaining, partially at least, a measure of the controlled conditions enjoyed in the laboratory. Accordingly, the "mouse-proof" experimental field has proven an effective method for studying populations. It appears that this technique has almost unlimited applicability to the study of the population dynamics of small mammals.

Care should be taken in the extrapolation to natural populations of conclusions based upon data obtained under artificial situations. The results discussed here, and the hypotheses suggested by them, may be functions of the experimental situation only.

Movement data

The frequency of moves to nest boxes during the last 7 days of the period of population establishment showed that between 55 and 65% of the mice moved to different nest boxes each night (Fig. 4). Although more than half of the mice moved to different nest boxes each night, less than half of these moves were to nest boxes previously unvisited by that mouse (Fig. 6). Therefore, while mice moved at a relatively constant rate, they moved less frequently to unvisited boxes, even though there were many available. Thus, each mouse localized (Fig. 5) to the use of a few nest boxes among which it continued to move.

The commonly accepted concept that an animal maintains one nest site around which its activity centers is contradicted by the evidence cited above. The idea of a single nest site has conceptual value in the explanation of territorial behavior in mammals (Burt 1940, 1948, p. 21). It may, however, lead to error when dealing with species in which such defense behavior is questionable (Blair 1940, 1951, 1953).

The fact that each mouse used an average of 4.3 nest boxes during the last 10 days raises 2 questions. Were these multiple residence sites only a function of the large number of boxes available or was each a home site or refuge? Howard (1949) studying natural populations of prairie deermice, found that mice living in areas with a large number of nest boxes changed their homesites more frequently than those living where nest boxes were more widely distributed. Since he visited his nest boxes only once a week, his experiments were not designed so that the number of nest boxes used per mouse could be ascertained. Nicholson (1941) studying the white-footed mouse (*Peromyscus leucopus noveboracensis*) in the wild, found that mice left the nest boxes after a "short period of residence." During his study, 174 mice were captured more than once in nest boxes. Of these only 16 lived in a box for more than 4 consecutive weeks. His data are of questionable significance in this comparison since he, too, inspected his boxes only once a week.

Blair (1940), studying prairie deermice, found that individuals fled to a number of different holes after their release from live traps. He concluded that each mouse had 6 or more refuges within its home range, of which an unknown number were permanent homes. His later study (1951) of the beach mouse (*Peromyscus polionotus leucocephalus*) indicated that the home range of each mouse contained an average of about 20 holes, of which a mean of 5 were entered by each after release from the traps. The fact that mice stored food and nested there for short periods indicated that these holes were more than refuge holes.

In the present study, the mice moved among approximately 5 nest boxes during the last 10 days of each experiment. In those experiments in which mice disappeared early in the experimental period, no increase was noted in the average number of nest boxes occupied by the remaining individuals. This may indicate that each mouse selected a relatively constant number of boxes to be used as refuges and/or nest sites. Since nest boxes were inspected only during the day, there was no way of distinguishing between nest sites and refuges. Nocturnal observations, however, indicated that nest boxes were used both for nest sites and refuges, depending upon the circumstances. As suggested by Burt (1940), it would be of distinct survival value for a mouse to have several nests distributed over the area.

An important difference between the conditions maintained in this study and wild conditions is that the experimental mice did not have young while in the field, although most of the females were pregnant at the end of each experimental period. Care of a litter and perhaps pregnancy, may result in the occupancy of fewer nest boxes.

The possibility should not be overlooked that the daily nest box inspection may have caused the mice to move to other nest boxes as frequently as they did. Inspecting the nest boxes seemed of little significance, however, since only 55 to 65% of the mice moved each day. The nest box inspections could not have caused the movement unless each examination affected each mouse differently each day.

If mice move between temporary residence sites, home ranges and artificial distribution measurements (Burt 1940, 1943, Blair 1940, 1941, Hayne 1949, Holenreid 1940, Mohr 1947, Stickle 1946) calculated on the basis of a few nights' sampling may be greatly in error.

Gregarious behavior

The experimental mice were found alone significantly more often than in combinations. Mice were found in bisexual pairs significantly more often than in any other type of combination. Mice were recorded in bisexual pairs significantly more often than expected by chance or than found in unisexual pairs. Thus, a preference was shown for occurrence alone in nest boxes and for combinations only as bisexual pairs.

The above data illustrate the expected attraction between animals of the opposite sex. The fact that mice of both social treatments occurred alone so frequently, however, was unexpected. Howard's nest box study (1949) suggested that deermice were infrequently found alone in nest boxes, but usually were found in bisexual pairs. Howard further noted that when the sex ratio was unequal, several mice of the more numerous sex were found simultaneously with the opposite sex. He does not, however, give frequencies or the exact time of the year for these data.

Nicholson's nest box study (1941) indicated that white-footed mice usually were found living singly. Associations with other mice were of short duration and combinations usually were as bisexual pairs. Nicholson's study further revealed that very few associations composed of the same sex were formed during the breeding season. Of those formed, all occurred at the extreme limits of the breeding season. The data reported in this study are similar to Nicholson's findings. Out of 23 combinations of the same sex, 14 occurred during the last experiment (October 31-November 21).

The data obtained in this investigation indicate that during the breeding season, prairie deermice usually are found alone, combine rarely in other than bisexual pairs, and very rarely occur in a nest box with an animal of the same sex. These data may differ from Howard's because of the seminatural conditions under which these experiments were carried out. Most groups found by Howard were composed of both parents with their offspring. This was impossible under the experimental procedures followed in this study and may have resulted in the differences.

Attraction between mice

Little information is available regarding the responsibility for establishing or terminating bisexual pair combinations. Trapping records have been used as evidence that males have a larger home range than females (Burt 1940, Blair 1940, 1942). *Peromyscus* males are thought to move about more and to greater distances than females (Burt 1940, Nicholson 1941, Blair 1942). Thus, males would pass through more home ranges of females than females would of males. It might be supposed that males would combine in home sites with females more frequently than the reverse. In this study, however, no significant difference was found as to which sex originated the bisexual pair or which left it first.

Examination of the pair combination data indicated that there was no difference between the sexes in the proportion found with the opposite sex at least once. Intensive examination of the pairing behavior of those individuals which combined at least once indicated that males combined with a significantly greater number of females than females did with males. Further, each male was recorded with females a significantly greater number of days than each female was recorded with males. There was no significant difference, however, between the sexes in the number of days each animal of one sex was recorded with each animal of the opposite sex.

When the data measuring succession of mice in the nest boxes were examined, it was determined that females succeeded males significantly more often than expected by chance. Males succeeded females less than expected. These differential rates of nest box succession may be a result of attraction between mice of the opposite sex so that they succeed each other because one sex was in the nest box the previous day or avoidance of animals of the opposite sex. The avoidance hypothesis suggests that succession was due to movement by a mouse away from a nest box because of invasion by a mouse of the opposite sex.

It is doubtful that the above data indicate an avoidance between opposite sexes since the number of bisexual pair combinations was larger than that of the other combinations. Also, general avoidance of the opposite sex would not have survival value to the species.

The special significance of the behavior noted above is that females succeeded males significantly more often than expected. These data indicate that females follow males into nest boxes on successive days more often than males do females. There was no evidence, however, that the females initiated the formation of bisexual pairs. Evidence on this point is obliterated by the fact that, of 116 records of the first day pairs were found together, 55 occurrences were in nest boxes in which neither mouse was recorded on the preceding day.

When the data were combined into categories assuming a tendency toward pairing (Table V) or avoiding or leaving combinations (Table IV), females exhibited a greater pairing tendency than males, and males exhibited a tendency to leave the nest box more and remain less often than females when an animal of the opposite sex came in.

The following hypothesis may be made regarding the pairing and breeding behavior of prairie deermice. Males combine with several females but females are more restrictive in their association with males. However, females may initiate the pairing behavior more than do males. This greater pairing tendency on the part of the female may be related to the estrus cycle and receptivity.

Repulsion between mice

Each mouse was found in only a few of the 24 nest boxes during each of the experiments. The average number of boxes occupied during the period of population establishment was 6.1 while only 4.3 nest boxes were occupied per mouse during the last 10 days. Since the records show that the mice were most often found alone and rarely combined in other than bisexual pairs, an apportioning of the nest boxes and perhaps the field by the mice is suggested.

As indicated earlier, the frequency of the occurrence of 2 animals of the same sex in a nest box was significantly less than expected by chance and monosexual pairs were recorded with significantly less frequency than bisexual pairs. In addition, there were significantly fewer records of animals of the same sex succeeding each other in nest boxes than were recorded for animals of the opposite sex. These data suggest that some type of negative force was operating to segregate mice of the same sex spatially. That this separation of like sexes is not merely a result of the lack of sexual attraction between such animals, but operates through some spatially or socially directed behavior pattern, is indicated by the low frequency with which animals moved into the nest boxes occupied on the previous day by like sex animals.

No conclusive information is available concerning the territorial behavior of prairie deermice, either in the defined sense of "defense of an area" (Noble 1939, Greenberg 1947) or in the less rigid and more dynamic sense discussed by Emlen (1957) and described by Davis (1958), Jenkins (1944) and Marler (1956). No studies of natural populations of the species *P. maniculatus* have reported active defense of a home area by the mice (Blair 1940, 1941, 1942, 1943, 1951, 1953, Dice 1932, Howard 1949). Territorial behavior has, however, been inferred from live trapping studies of *Peromyscus leucopus* (Burt 1940, 1949).

Some evidence of a "dynamic" non-aggressive type of behavior leading to an apportioning of the area among animals of the same population was collected through direct observations and by the homing test.

Observations made during the preliminary experiments as well as during the experimental periods discussed here indicate that when 2 animals met in the field, both jumped and ran away from each other. Occasionally, one mouse chased another a short distance. Observations of social interaction between residents and aliens while aliens were tethered at the feeding stations or at the home nest sites of residents, indicated that residents predominately avoided or ignored the aliens. In the few cases when the resident attacked the aliens, the attacks were of short duration and were terminated by the residents leaving the area. Laboratory studies (King 1957) of *P. m. bairdii* showed single males to be relatively nonaggressive toward other males. Terman (1958) found single females to be slightly more aggressive than single males when aliens were placed in their home mouse boxes. The incidence of attacks was very low for both sexes, however. When these same males and females were paired and aliens were then placed in their mouse box, the number of attacks by residents greatly increased and the males usually were the attackers. Such aggression by the male was usually of short duration. In these laboratory experiments, neither the resident or the alien could leave the mouse box, so fighting typically was terminated by the alien assuming a defense position and the resident hesitating to attack.

In the experiments in the field, however, the residents were free to leave the area, and did so.

The results of the homing experiments (Terman 1959) with aliens in the experimental field further elucidate this problem. Homing by residents to nest boxes in which young alien mice were retained was significantly less than that observed before the aliens were placed in the nest boxes. Avoidance of aliens was further demonstrated by the occurrence of the mice in empty nest boxes significantly more often than in boxes occupied by aliens. These data indicate that spatial distribution may be effected through avoidance or some unmeasured negative force between animals (Howard 1949). Prior occurrence (Braddock 1949) or merely presence in the area may be the important factors.

With regard to the question of territoriality, then, no reliable evidence for active defense of an area was shown. Animals of the same sex may be spatially segregated as a result of a negative repulsive force, hypothetically, avoidance.

SUMMARY

Factors influencing the geographical distribution of a species are effective through the local population. This study combined laboratory and field techniques in order to examine behavioral patterns affecting spatial distribution of mice under semi-natural conditions.

Successive populations of prairie deermice were raised from weaning age (21 days) in isolation or in groups. At 10 weeks of age, 4 bisexual pairs from each social treatment were systematically released into different one-half acre "mouse-proof" plots. The mice remained in the plots for 3 weeks during which their daily occurrence in nest boxes was recorded.

The "mouse-proof" field proved to be an effective method for the study of population dynamics under semi-natural conditions while maintaining a measure of the controlled conditions which are possible in the laboratory.

The following are phenomena noted which may be specific to populations of prairie deermice, to mice of the species *Peromyscus maniculatus,* or which may have general significance to small mammal populations:

(a) Between 55 and 65% of the mice moved to different nest boxes during the last 7 days of each period of population establishment. During that time, less than one-third of the mice moved to nest boxes previously unvisited by the mouse moving. As the experimental period progressed, an increasing daily proportion of those mice which moved did so to nest boxes in which they had previously been recorded. During the last 10 days of each period of population establishment, each mouse was recorded in an average of 4.3 nest boxes of the 24 available. Therefore, each mouse localized and used a few nest boxes among which it continued to move. These data indicate that each mouse maintained several refuges and/or nest sites rather than a single one around which its activity centered. Such behavior should be considered when measurements are made of the spatial patterns of individual animals in the wild.

(b) During the breeding season, the prairie deermice in this study were usually found alone or in bisexual pairs, combined rarely in other than bisexual pairs, and very rarely occurred in a nest box with an animal of the same sex.

(c) No conclusive evidence was obtained as to which sex originated or terminated bisexual pairs.

(d) Mice of opposite sex succeeded each other in nest boxes significantly more often than those of the same sex. Females followed males into nest boxes on successive days significantly more often and males followed females significantly less often than expected by chance.

(e) No reliable evidence for territoriality as defense of an area was obtained. The data, however, indicate that each population was spatially distributed in a pattern mutually realized by the individuals of the population. Animals of the same sex may be spatially segregated as a result of a negative repulsive force, hypothetically, avoidance.

ACKNOWLEDGMENTS

The author wishes to express his sincere appreciation to Dr. John A. King, Roscoe B. Jackson Laboratory, Bar Harbor, Maine, who provided facilities, invaluable suggestions and criticisms without which this study would have been impossible. Grateful acknowledgments also are due to Dr. Don W. Hayne, Institute for Fisheries Research, Michigan Department of Conservation and to Dr. James C. Braddock, Zoology Department, Michigan State University, for stimulating suggestions and criticisms throughout this study; to Dr. Charles D. Richards, Department of Botany and Plant Pathology, University of Maine, who made final identification of the plants collected. Sincere thanks are due Dr. Karl A. Stiles, Head, Department of Zoology, Michigan State University, and to Dr. John Paul Scott and Dr. John L. Fuller, Roscoe B. Jackson Laboratory for their cooperation in the arrangements whereby this study was undertaken as part of the author's graduate program.

REFERENCES

Blair, W. F. 1940. A study of prairie deer-mouse populations in southern Michigan. Amer. Midl. Nat. **24**: 273-305.

———. 1941. The small mammal populations of a hardwood forest in northern Michigan. Contr. Lab. Ver. Biol. Univ. Mich. **17**: 1-10.

———. 1942. Size of home range and notes on the life history of the woodland deer-mouse and eastern chipmunk in northern Michigan. Jour. Mamm. **23**: 27-36.

———. 1943. Populations of the deer-mouse and associated small mammals in the mesquite association of southern New Mexico. Contr. Lab. Vert. Biol. Univ. Mich. **21**: 1-40.

———. 1951. Population structure, social behavior, and environmental relations in a natural population of the beach mouse (*Peromyscus polionotus leucocephalus*). Contr. Lab. Vert. Biol. Univ. Mich. **48**: 1-47.

———. 1953. Population dynamics of rodents and other small mammals. Advances in Genetics **5**: 2-37.

———. 1956. The species as a dynamic system. The Southwestern Naturalist **1**: 1-5.

Braddock, J. C. 1949. The effect of prior residence upon dominance in the fish *Platypoecilus maculatus*. Physiol. Zool. **22**: 161-169.

Brand, R. A. 1955. Abundance and activity of the woodmouse (*Peromyscus leucopus noveboracensis*) in relation to the characteristics of its habitat. Ph.D. Thesis, Univ. of Michigan.

Brown, R. Z. 1953. Social behavior, reproduction, and population changes in the house mouse (*Mus musculus* L.). Ecol. Mono. **23**: 217-240.

Burt, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Misc. Pub. Mus. Zool. Univ. Mich. **45**: 1-58.

———. 1943. Territoriality and home range concepts as applied to mammals. Jour. Mamm. **24**: 346-352

———. 1948. The mammals of Michigan. Ann Arbor, Univ. Mich. Press.

———. 1949. Territoriality. Jour. Mamm. **30**: 25-27.

Calhoun, J. B. 1948. Mortality and movement of brown rats (*Rattus norvegicus*) in artificially supersaturated populations. Jour. Wildl. Mgt., **12**: 167-172.

———. 1949. A method of self-control of population growth among mammals living in the wild. Science **109**: 333-335.

———. 1950. The study of wild animals under controlled conditions. Annals New York Academy Sci. **51**: 1113-1122.

———. 1952. The social aspects of population dynamics. Jour. Mamm. **33**: 138-159.

———, **and W. L. Webb.** 1953. Induced emigrations among small mammals. Science **117**: 358-360.

Clark, F. 1938. Age of sexual maturity in mice of the genus *Peromyscus*. Jour. Mamm. **19**: 230-234.

Crowcroft, P. 1955. Territoriality in wild house mice, *Mus musculus* L. Jour. Mamm. **36**: 299-301.

Davis, D. E. 1958. The role of density in aggressive behavior in house mice. Anim. Behav. **6**: 207-211.

——— **and J. J. Christian.** 1956. Changes in Norway rat populations induced by introduction of rats. Jour. Wildl. Mgt. **20**: 378-383.

Dice, L. R. 1932. The prairie deer-mouse. Bull. Cranbrook Inst. Sci. **2**: 1-8.

——— **and R. M. Bradley.** 1942. Growth in the deermouse, *Peromyscus maniculatus*. Jour. Mamm. **23**: 416-427.

Emlen, J. T. 1957. Defended area—A critique of the territory concept and of conventional thinking. Ibis **90**: 352.

Greenberg, B. 1947. Some relations between territory, social hierarchy, and leadership in the green sunfish (*Lepomis cyanellus*). Physiol. Zool. **20**: 267-299.

Hayne, D. W. 1949. Calculation of size of home range. Jour. Mamm. **30**: 1-18.

Holdenried, R. 1940. A population study of the long-eared chipmunk (*Eutamias quadrimaculatus*) in central Sierra Nevada. Jour. Mamm. **21**: 405-411.

Howard, E. 1920. Territory in bird life. London, John Murray.

Howard, W. E. Dispersal, amount of inbreeding, and longevity in a local population of prairie deermice on the George Reserve, southern Michigan. Contr. Lab. Vert. Biol. Univ. Mich. **43**: 1-50.

Jenkins, D. W. 1944. Territory as a result of despotism and social organization in geese. Auk **61**: 30-47.

King, J. A. 1957. Intra- and interspecific conflict of *Mus* and *Peromyscus*. Ecology **38**: 355-357.

——— **and B. E. Eleftheriou.** 1957. Effects of social experience in the laboratory upon adaptation of *Peromyscus* to a natural environment. Anat. Rec. **128**: 576.

Marler, P. 1956. Studies of fighting Chaffinches. (3) Proximity as a cause of aggression. Brit. Jour. Anim. Behav. **4**: 23-30.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. Amer. Midl. Nat. **37**: 223-249.

Nice, M. M. 1941. The role of territory in bird life. Amer. Midl. Nat. **26**: 441-487.

Nicholson, A. J. 1941. The homes and social habits of the wood mouse (*Peromyscus leucopus noveboracensis*) in southern Michigan. Amer. Midl. Nat. **25**: 196-223.

Noble, G. K. 1939. The role of dominance in the life of birds. Auk **56**: 263-273.

Orgain, H. and M. W. Schein. 1953. A preliminary analysis of the physical environment of the Norway rat. Ecology **34**: 467-473.

Provost, M. W. 1940. Dynamics of *Peromyscus* populations. M. S. thesis. Univ. N. H.

Schneirla, T. C. 1950. The relationship between observation and experimentation in the field study of behavior. Annals N. Y. Acad. Sci. **51**: 1022-1045.

Scott, J. P. 1944. Social behavior, range and territoriality in domestic mice. Proc. Ind. Acad. Sci. **53**: 188-195.

———. 1950. The social behavior of dogs and wolves: an illustration of sociobiological systematics. Annals N. Y. Acad. Sci. **51**: 1009-1021.

———. 1956. The analysis of social organization in animals. Ecology **37**: 213-221.

Stickle, L. F. 1946. The source of animals moving into a depopulated area. Jour. Mamm. **27**: 301-307.

Strecker, R. L. 1954. Regulatory mechanics in house mouse populations—the effect of limited food supply on a confined population. Ecology **34**: 375-385.

Terman, C. R. 1958. A laboratory study of area defense in *Peromyscus maniculatus bairdii*. Unpublished.

———. 1959. Social factors influencing spatial distribution in populations of prairie deermice. Ph.D. Thesis, Michigan State Univ.

INSECT-VEGETATION RELATIONSHIPS IN AN AREA CONTAMINATED BY RADIOACTIVE WASTES[1]

D. A. Crossley, Jr. and Henry F. Howden
Health Physics Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee and Entomology Research Institute, Department of Agriculture, Ottawa, Canada

Introduction

The role of herbivorous insects in the biological cycling of radioactive materials has received little attention, despite recent interest in the bioaccumulation of fission products. Much work has been done on the soil to plant transfer of radioisotopes, but most of the investigations on consumers have been concerned with animals in the food chain leading directly to man. There is a need for information on the effect of natural populations of consumer animals on biological cycling, particularly of radioactive materials arising from weapons fallout or radioactive waste disposal operations.

With the draining of White Oak Lake in October 1955, a unique opportunity was created for the study of a biological system into which radioactive isotopes and fission products would become incorporated. White Oak Lake served as a final holding basin for the Oak Ridge National Laboratory's low-level radioactive wastes for approximately 12 years. Upon drainage, approximately 35 acres of contaminated alluvial terrain was exposed. Soil surveys indicated concentrations of about 0.6 curies per acre of Strontium-90 and 11 curies per acre of Cesium-137, as well as significant concentrations of Cobalt-60, Cerium-144, and Ruthenium-106. Plant invasion of this area began in April 1956, and shortly thereafter insect associates of the vegetation appeared. The resulting ecosystem on White Oak Lake bed may be envisioned as a gigantic radioactive tracer experiment, which can yield information of interest to both ecologists and health physicists. From the ecological viewpoint, the radioisotopes serve as tracers by means of which the dynamics of ecosystems may be investigated. The health physicist is interested in the movement through food chains of such radioisotopes as Strontium-90 and Cesium-137. Studies on White Oak Lake bed have been conducted with these two general areas of interest in mind.

The specific objectives of the work reported in the present paper were: (1) to discover which species of insects would invade the lake bed vegetation, (2) to estimate the biomass of these insects, and (3) to obtain gross data on the uptake of fission products by the insects. The successful completion of these objectives provided data with which a first approximation of the turnover of Cesium-137 by insects may be made. The isotopes themselves provided information on consumption of plants by the insects. These results provide an initial appraisal of the role of herbivorous insects in the biological cycling of radioactive materials.

The sampling program was designed to give an estimate of the role of the insects in the environmental cycling of the radioactive fission products, and was not concerned with effects of radiation upon the insect populations. Presumably the presence of radiation fields could affect the succession of insects or the population sizes which might develop but no obvious signs of this were noted during the course of the survey. The average air dose-rate 5 cm above the ground was about 15 mr/hr (Lee and Auerbach 1959). Continuous exposure throughout the growing season would produce doses of about 40 r, far below those used to produce gross somatic effects on insects in laboratory experiments (Hassett and Jenkins 1952). Deformities, such as reported for *Onthophagus* (Howden 1957) and *Trogoderma* (Howden and Auerbach 1958), were not observed in insects collected from White Oak Lake bed. The

---

[1] Research performed in the Health Physics Division of the Oak Ridge National Laboratory, operated for the U. S. Atomic Energy Commission by Union Carbide Corporation.

radiation dosage from internally deposited isotopes in the insects may exceed the external dosage; however, it seems unlikely that the radiation would produce any but very subtle effects on the parameters investigated.

Vegetational History

White Oak Lake bed lies in the western end of Melton Valley (Bethel Valley Quadrangle of the U. S. Geological Survey) between low ridges which are near the Clinch River (Figure 1). Of the 35 acres of lake bottom exposed, a study area of about 2.5 acres was selected in the lower lake bed and was marked in a permanent grid with metal stakes 10 meters apart. Vegetational succession and associated insects were studied in the gridded area and in the adjacent area directly across White Oak Creek (Figures 2, 3). Plant invasion of the bed started early in the spring of 1956. During the summer of 1956, 78 species in 31 families of flowering plants were identified by Shanks and DeSelm (1956). However, only 2 groups dominated the vegetation: smartweed (*Polygonum* spp.) and sedge-rush (*Carex* spp., *Cyperus* spp., *Juncus* spp.). Fig. 2 illustrates the distribution of these species in August of 1956. The central portion of the bed contained predominantly smartweed, especially *Polygonum lapathifolium* L. Areas of bare ground also existed. The outer edge of the lake bed was well covered by areas of sedge-rush mixture, as well as areas of mixed forbs containing the greatest concentration of plant species.

By 1957, willows (*Salix nigra* Marsh.) had become a conspicuous element of the community (Fig. 3), both on the north side of White Oak Creek and just south (not shown in Fig. 3) of the gridded area. While the smartweed and sedge-rush associations still covered a large area, they were not as prominent as in the previous year. The complex of species which had existed in the previous year only at the outer edge of the study area was extended now almost to White Oak Creek. The abundant forbs included jewelweed (*Impatiens pallida* Nutt., *I. capensis* Meerb.) along the bank of the creek, eupatorium (*Eupatorium serotinum* Michx.) as scattered individuals in the central gridded portion, and beggar-tick (*Bidens frondosa* L.) scattered in the central portion. However, only smartweed, sedge-rush, and willow associations were sufficiently extensive to permit satisfactory quantitative sampling for insects.

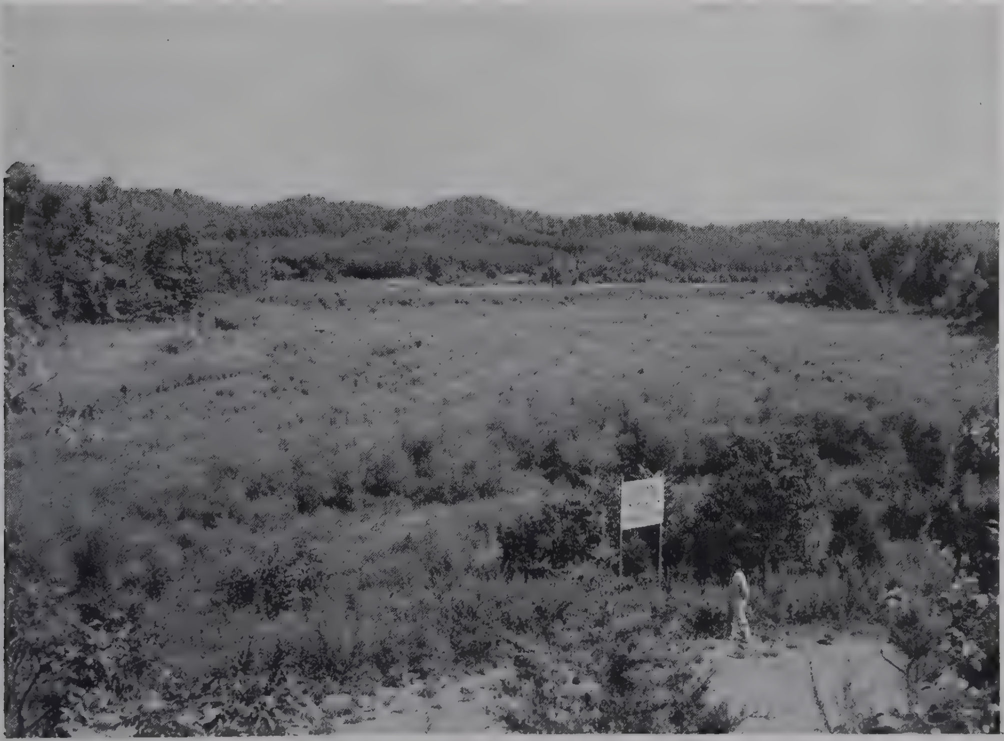

Fig. 1. White Oak Lake bed: August, 1958.

In the summer of 1958, the sedge-rush association was about as extensive as in 1957, although it was infiltrated with grasses on the margins of the lake bed. The willows continued to extend their coverage of the lake bed. The smartweed association, however, was virtually absent. Except for a small band of smartweed which developed along White Oak Creek, smartweed occurred only as scattered individuals among the mixed forbs.

METHODS

A number of sampling procedures were considered, particularly those mentioned by Hoffmann *et al.* (1949). The most practical method for our purposes proved to be a system of replicated sweeps with an insect net, the results of which were checked against the yields from a box trap covering one square meter. Cross (1956) used a similar method for the quantitative estimation of insect populations.

The sweep net sampling was based on a series of 10 consecutive rapid sweeps in the top part of the vegetation being sampled. A net with a 4-ft handle and a 14-in. diameter nylon marquisette collecting net was used.

The box trap (Figure 4) was a portable plywood box standing 5 ft high and open at the bottom, which covered a square meter. On one side was a plastic funnel, to which a pint jar could be attached. When the box was dropped over the vegetation, many insects were attracted to the light visible through the plastic funnel and were collected in the jar. After 2 or 3 hours of operation a small trap door opposite the funnel was opened and the vegetation within the box was swept with a small net. Frequently, the vegetation in the box was clipped and brought into the laboratory for examination.

Table I compares the box trap with sweep net collections by 2 investigators. The results tabulated for the box trap show only those insects which were attracted to the trap jar; additional orthopterans and hemipterans were taken subsequently by sweeping inside the box. These data show that many minute insects escaped through the net. Of the 582 insects taken in the box trap, 319 were minute insects (midges and chalcids). If these minute insects are not considered for either box trap or sweep net methods, it appears that the 10-sweep method gives a reasonable approximation of the number of insects on one square meter of vegetation.

While the box trap method was the more reliable, it required several hours of operation in the

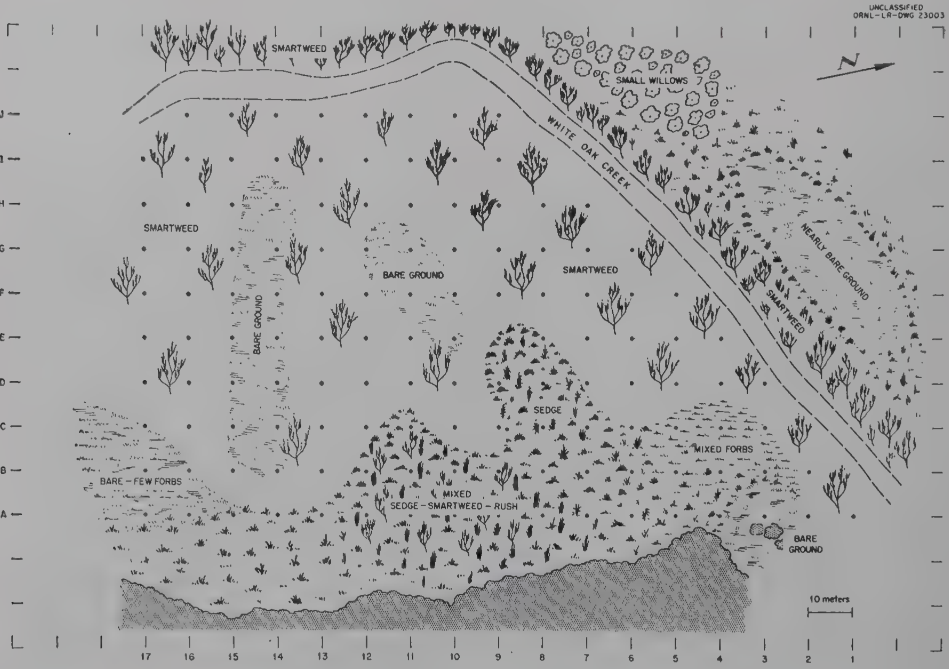
UNCLASSIFIED
ORNL-LR-DWG 23003
N
SMARTWEED
SMALL WILLOWS
WHITE OAK CREEK
NEARLY BARE GROUND
SMARTWEED
SMARTWEED
BARE GROUND
BARE GROUND
SMARTWEED
SEDGE
MIXED FORBS
MIXED
SEDGE – SMARTWEED – RUSH
BARE – FEW FORBS
BARE
GROUND
10 meters
J
I
H
G
F
E
D
C
B
A
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1

FIG. 2. White Oak Lake bed, Ecology study area. Distribution of vegetation, August 1956.

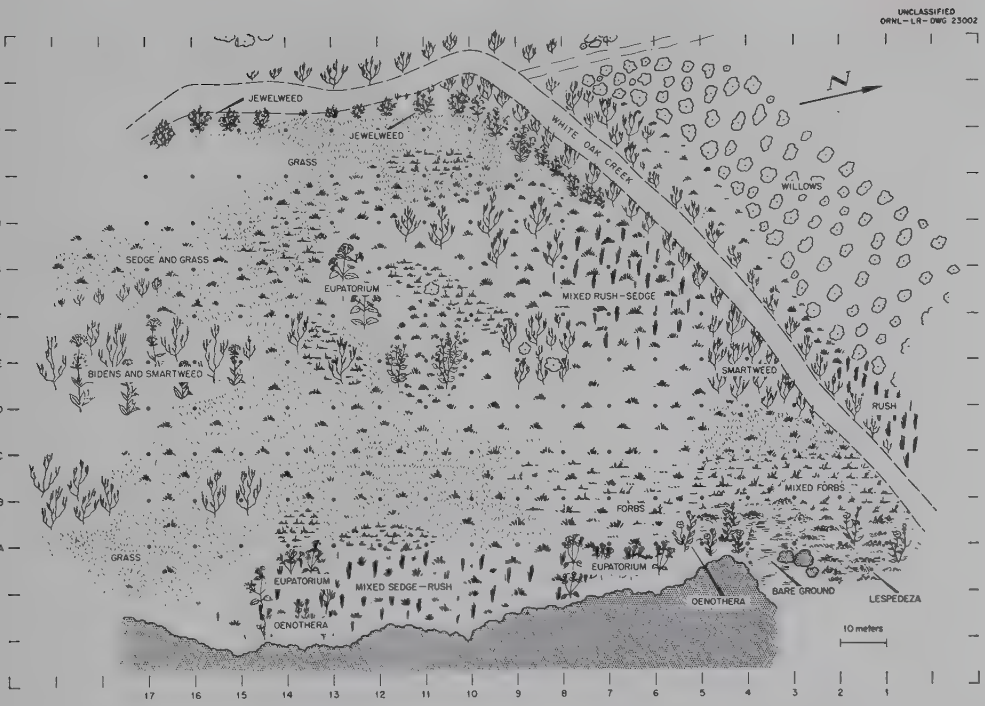
UNCLASSIFIED
ORNL-LR-DWG 23002
N
JEWELWEED
JEWELWEED
GRASS
WHITE OAK CREEK
WILLOWS
SEDGE AND GRASS
EUPATORIUM
MIXED RUSH-SEDGE
BIDENS AND SMARTWEED
SMARTWEED
RUSH
MIXED FORBS
FORBS
GRASS
EUPATORIUM
EUPATORIUM
MIXED SEDGE-RUSH
OENOTHERA
OENOTHERA
BARE GROUND
LESPEDEZA
10 meters
J
I
H
G
F
E
D
C
B
A
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1

Fig. 3. White Oak Lake bed, Ecology study area. Distribution of vegetation, July, 1957.

Table I. Comparison of box trap and sweep net collections (total of 5 trapping periods in sedge and smartweed areas in June 1957)

Insect Group	Box Trap	Sweep Net	
		Collector No. 1	Collector No. 2
Hymenoptera	197	16	27
(chalcids alone)	(141)	(0)	(0)
Coleoptera	32	16	42
Homoptera	85	106	91
Hemiptera	17	45	88
Diptera	249	70	101
(midges alone)	(178)	(58)	(95)
Orthoptera	2	34	40
Totals	582	287	389

field in order to obtain a sample. Where several different areas must be sampled on the same day and at the same time of day, the 10-sweep method is the more practical. The box trap was not used extensively until 1958, so that results in the present paper are based primarily on the 10-sweep method.

Results of the 10-sweep method were subject to influence by the individual collectors. As can be seen from Table I, collector No. 2 caught more insects than did collector No. 1. It was necessary for the collectors to work together in the field and develop similar methods of handling the sweep net. The box trap provided a baseline against which sweep-net results could be compared. However, the collectors had difficulty in adjusting their netting methods to obtain results which were similar. This difficulty was partially overcome by restricting population samples to one collector (No. 1) and biomass samples to the other (No. 2).

A third collecting method, consisting of empty cans sunk in the ground to form a grid, yielded a number of ground beetles. However, these collections could not be related to a unit area basis and were therefore not used in the regular sampling procedure.

Only the dominant vegetation types were sampled, namely smartweed, sedge-rush, and (in 1957 and 1958) willow. Two similar areas were sampled in each vegetation type. For smartweed and sedge-rush, one area each in the gridded area and one each across the creek were sampled. These were referred to as "inshore" and "center," respectively. The center areas were those closer to the creek. For willow, one area across the creek from the gridded area ("center") and one area south of the gridded area (inshore") were sam-

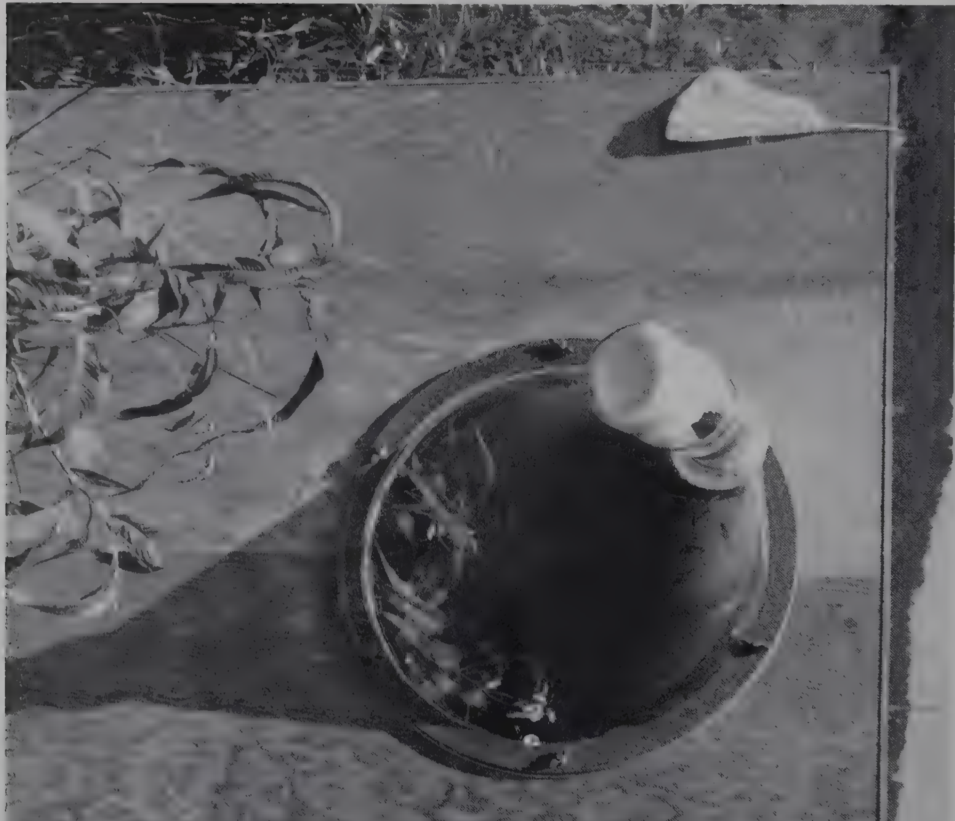

FIG. 4. Box trap for insects, in use in smartweed area.

pled. Duplicate 10-sweep samples were taken in each sampling area. One sample of the pair was used for estimates of dry weight of herbivores and predators (biomass). The other sample was retained for identification of species and counts of individuals.

Systematic sampling in 1956 did not begin until the latter part of the summer. Thus, no quantitative estimates of the insect populations are available until August. Six 10-sweep samples were taken at weekly intervals from August 2 to September 4, in each of 4 vegetation types (sedge-rush inshore, sedge-rush center, smartweed inshore, and smartweed center). In 1957, systematic sampling of the insects on vegetation was carried on for 14 consecutive weeks, from June 3 to September 3. Six vegetation types were sampled each week (inshore and center areas of sedge-rush, smartweed, and willow). By the summer of 1958, the willows had greatly increased in coverage and had reached such a height that accurate sampling was impossible. The smartweed and sedge-rush associations were infiltrated by many forb species. Taxonomic and biomass samples were taken but at less frequent intervals than in the preceding years. Less attention was given to the identification of insect species, in order that more effort could be placed on estimates of the biomass and radioactivity.

The samples were sorted in the laboratory to major groups, counted and then small samples of each species were mounted and sent to specialists for identification. Upon return of identified material the more easily determined and common species, particularly those associated with one of the dominant plants, were counted. It was not possible to attempt to identify and do complete counts of all of the individuals for each species. We did attempt to have representatives of each species identified by a specialist.

Samples taken for estimates of insect biomass were sorted in the laboratory, dried at 105°C, weighed, and then counted for radioactivity. A Model 810 Baird-Atomic gamma scintillation detector with a 2 × 2 inch well crystal was used for measurement of gamma radiation. Spectrometric measurements of Cesium-137 and radiochemical measurements of Strontium-90 in insect samples were performed by the Analytical Chemistry Division, Oak Ridge National Laboratory.

Biomass of the Insects

Weights of samples

Samples for estimation of the insect biomass were taken at weekly intervals during August-September, 1956, June-September of 1957, and irregularly during 1958. These were both 10-sweep samples with an insect net and box trap samples. The results are given in Table II, which shows the biomass for the 3 years in each of the 3 vegetation types. From these data the biomass of insects was estimated to be approximately 200-300 mg/m^2 in the herbaceous vegetation and sedge-rush areas, and 100 mg/m^2 in the willow areas. The apparent increase from 200 mg in 1957 to 300 mg in 1958 may not be real, since the more efficient box trap method was used extensively in 1958. The large standard errors attached to the estimates suggest that better sampling methods are needed if differences between years are to be demonstrated.

Table II. Biomass (mg/m^2) of insects on White Oak Lake bed vegetation. Shown are $\bar{x}$, the mean biomass for n samples, and the standard error of the mean

Year	Sedge-Rush			Smartweed			Willow		
	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n
1956	—	—	—	192	38	3	—	—	—
1957	197	34	22	202	26	22	88	9	22
1958	273	78	6	330	92	6	—	—	—

Biomass samples included spiders when the samples were taken with the sweep nets. Spiders were not weighed separately but were included with the insect biomass, since spiders occur on the foliage with the insects and are important predators of insects. In the weights of predators given below spiders are included; about 50% of the predators collected were spiders.

Within a season, biomass estimates showed no tendency to increase or decrease with time. The best data are those for 1957, when each area was sampled at weekly intervals. The only trend that could be detected in the 1957 data was in the willow samples, where increases in weight of total insects were sometimes associated with emergences of numbers of adult willow flea beetles.

The "center" and "inshore" replicates taken each week showed a remarkable similarity in estimates of biomass for the willow areas. A correlation coefficient (r) of 0.94 (highly significant) was calculated for the samples from the 2 willow areas. However, correlation coefficients for "center" and "inshore" replicates from the sedge-rush and smartweed areas were 0.01 and 0.26, and were not significant statistically. The high correlation between replicates in the willow areas seemingly was the result of emergences of adult willow flea beetles. The lack of correlation in sedge-rush and smartweed replicates is further evidence that fluctuations in estimates of weekly biomass were not related to any simple seasonal trend.

Comparisons of weights and numbers

Weights of samples were compared with numbers of insects in the samples in an attempt to (a) derive an expression for predicting the weights of samples from the total number of insects in the sample, and (b) explain some of the large variation in sample weights. A correlation coefficient (r) for sample weights vs. number of insects per sample was 0.26 for herbivores only. This value is significant statistically ($P < 0.05$) but is so small as to suggest that weights cannot be predicted satisfactorily from numbers, in such samples of mixed species. Tabulation of the insects in these samples by insect orders showed no evidence of marked influence on weight by any one order. The presence of several orthopterans, for example, might tend to produce a heavier sample than predicted by numbers alone. However, tabulation showed that the weights of samples were independent of the number of orthopterans present. Evidently, the deduction of sample weights from numbers of insects would require a rather detailed analysis of the samples.

Herbivores and predators

In the 1957 biomass samples the herbivores and predators were sorted and weighed separately. The means given in Table II for 1957 can be broken down into: Sedge-rush, 161 mg herbivores, 36 mg predators; Smartweed, 169 mg herbivores, 33 mg predators; Willow, 76 mg herbivores, 12 mg predators. Predators thus account for 13 to 18% of the total insect biomass for 1957. Data for 1956 are incomplete but the percentages of predators are similar to those for 1957. Weights of predators and weights of herbivores showed considerable sampling variation from week to week, as did the total insect biomass, but no trend toward an increase or decrease with time could be detected. For insects from smartweed in 1957, the coefficient of variation for the total biomass was 43%, that for herbivores alone was 66% and that for predators alone was 54%. Thus the samples of predators, although smaller, had about the same percentage variation as did the herbivore samples. The tabulated data gave no indication that variation in weekly weights of predators was unduly influenced by any single large species (for example, *Polistes* spp.).

Herbivore-to-predator ratios (numbers of individuals) in the 1957 samples were: Smartweed inshore, 6.2; smartweed center, 5.8; sedge-rush inshore, 2.8; sedge-rush center, 3.2; willow inshore, 7.1; willow center, 7.0. Herbivore-to-predator ratios for biomass were: Smartweed, 5.1; sedge-rush, 4.5; willow, 6.3.

ACCUMULATION OF RADIOACTIVE ISOTOPES BY THE INSECTS

Early in these studies, estimates of the gamma radioactivity of the biomass samples showed that the insects were accumulating measurable quantities of radioactive nuclides from their environment. As the studies progressed it became obvious that the survey methods used could provide only a gross estimate of the quantitative role of insects in the biological cycling of the fission products. One difficulty was that the biomass samples were too small to permit identification of the specific radionuclides without laborious radiochemical procedures. Since several gamma-emitting nuclides were known to be present in the soil, no assumptions could be made as to what nuclides and in what proportions might be present in the insects (more recently, Cs^{137}, Co^{60}, Ru^{106}, and Zr^{95}-Nb^{95}, as well as Sr^{90} have been found in insects from White Oak Lake bed). Total gamma radioactivity of smaller samples, recorded as counts per minute, has value only for comparisons between areas.

Larger collections of insects taken in September, 1958, have been analyzed by gamma spectrometry for Cs^{137} and radiochemically for Sr^{90}.

Radioactivity of the biomass samples

Many but not all of the biomass samples had gamma counting rates higher than background. Twenty-one of the 22 herbivore samples from the smartweed area and 12 each of the 22 from the willow area and sedge-rush area had counting rates significantly higher than instrument background counting rates. In the smartweed areas, count rates were from 11 to 154 counts per minute above background (instrument background averaged about 200 cpm.) In each of the areas, only 1 or 2 of the 22 predator samples were higher than background but fewer significant count rates would be expected since the predator samples were much smaller than the herbivore samples. It is difficult to place any interpretation on these results since samples varied in size as well as in count rates. The results do suggest that there were no overwhelming differences in isotope concentrations between insect samples from the different vegetation types.

No increase in count rate as a function of time could be seen. Since known elimination rates for isotopes from insects are high (Crossley and Pryor 1960) little change might be expected, provided that plant concentrations and insect feeding rates changed little throughout the season. Indeed, the lack of seasonal variation in insect biomass and in the accumulated radioactivity suggests that plant uptake and insect feeding rates remained essentially constant during the summer months.

Radionuclide concentrations in insects and plants

Results of analyses for Cs^{137} and Sr^{90} in the insect samples taken in September, 1958, are shown in Figures 5 and 6. Concentrations in the host plant leaves are shown also. Food relationships for these insects are not clear-cut. In each case the host plant species listed is that from which the insects were actually taken.

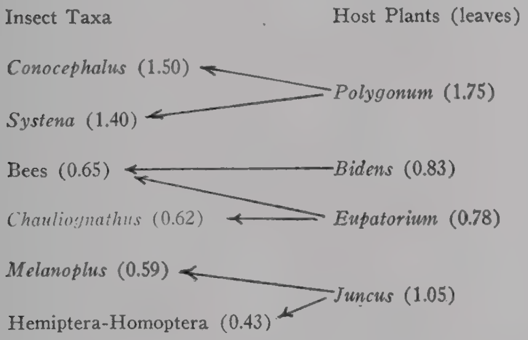

FIG. 5. Transfer of Sr^{90} from plants to insects. Values are $\mu c \times 10^{-4}$ per gram dry wt.

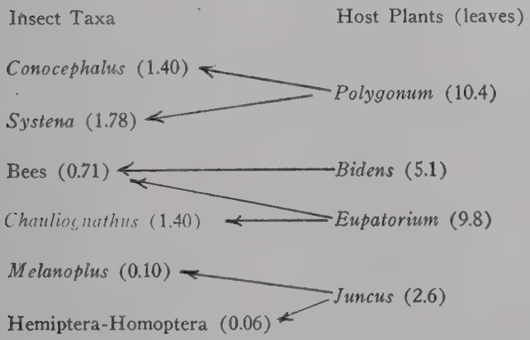

FIG. 6. Transfer of Cs^{137} from plants to insects. Values are $\mu c \times 10^{-4}$ per gram dry wt.

In general, the radionuclide concentrations in the insects are related to concentrations in the host plants. That is, those insects feeding upon plants with higher concentrations have higher concentrations themselves. Some exceptions occur, for example, in insects presumably obtaining Cs^{137} from *Juncus*. However, it seems remarkable that any such relationships can be demonstrated in view of the diverse feeding habits of the insect species involved.

These figures show that concentrations of Cs^{137} in insects are almost as high as in plant tissues (Fig. 6). Typically, insect concentrations are about 70% of concentrations in plants. By contrast Sr^{90} concentrations in insects are almost exactly an order of magnitude lower than those in plant tissues (Fig. 5). This difference may result from differing rates of elimination for the isotopes (Crossley, unpublished data). Strontium appears to be eliminated more rapidly than cesium and, as a result, equilibrium values for strontium in insects are much lower than the concentrations in food plants. It is interesting that a Cs^{137}/Sr^{90} ratio of almost 20:1 in the soil and about 1:6 in plant leaves resulted in about a 1:1 ratio of the 2 radionuclides in the insect population.

Radionuclides in insects in relation to the food chain

A gross evaluation of the role of insects in the biological cycling of the fission products may be based upon the data presented above in combination with recent soil and plant data.

Table III shows the concentrations of Sr^{90} and Cs^{137} in the soil and 3 trophic levels (plant, herbivore, carnivore), on both per unit weight and per unit area bases. Soil and plant estimates in this table are based upon data reported by Auerbach for the lower lake bed (Auerbach 1959). Soil values are averages for a number of samples. Per unit area concentrations for soils are the per unit weight values times a factor (1.64×10^3, based on 100 6-in. cores) obtained from soil mass samples. Per unit weight concentrations in plant leaves are averages for the herbaceous species. Per square meter concentrations in plants are based upon harvests on 6 half meter quadrats in the lower lake bed and include values for total plants rather than leaves alone. Insect concentrations are averages for all available data. Only a few values were available for predaceous insects; these fall within the range for herbivores and are not significantly different from them. Per area concentrations in insects are the per unit weight concentrations time the biomass.

Per unit weight concentrations show some reduction in movement through the food chain, but Sr^{90} concentrations in the predaceous insects are still about 25% of the soil concentrations. Cs^{137} concentrations are about 1% of soil concentrations. In the Sr^{90} chain the major reduction in concentration occurs at the plant-insect step; in the Cs^{137} chain this reduction occurs at the soil-plant step. Reduction does not necessarily occur at each transfer; plant leaves have higher Sr^{90} concentrations than the soil. Expressed as concentrations per unit weight, transfer of Sr^{90} and Cs^{137} is fairly efficient.

TABLE III. Concentrations of Sr^{90} and Cs^{137} in soil and trophic levels of the White Oak Lake bed system

	Concentrations Per Gram (μc/100 g dry wt)	
	Sr^{90}	Cs^{137}
Soils	0.036	0.73
Plants (leaves)	0.12	0.018
Insects:		
Herbivores	0.0091	0.0087
Predators	0.0081	0.0097
	Concentrations Per Unit Area μc/m²	
	Sr^{90}	Cs^{137}
Soils	60	1.2×10^3
Plants (total)	3.3×10^{-1}	5.5×10^{-2}
Insects:		
Herbivores	2.1×10^{-5}	2.2×10^{-5}
Predators	3.1×10^{-6}	3.7×10^{-6}

When concentrations are expressed on a per unit area basis (bottom of Table III), significant reduction in amount occurs at each transfer. Between soils and insects, reductions of several orders of magnitude are involved.

DISCUSSION OF BIOMASS AND TURNOVER OF RADIONUCLIDES

The estimate of 200-300 mg dry wt of insects per square meter seems small, but it compares very favorably with that reported by Cross (1956) for old fields in early successional stages on the AEC Savannah River Plant Reservation located on the Upper Coastal Plain of South Carolina. Cross's values ranged upwards to 300 mg/m² of herb stratum insect herbivores for the richer old fields. Evidently very few studies on the biomass of natural insect communities have been done, although a number of reports on the densities of economic insects are available and weight relationships are known for single species (Wolcott 1937). Of course, our figures (as well as those of Cross) do not include all the biomass of herbivorous insects since borers, miners, root-feeders and others were not sampled adequately.

Productivity is of greater interest than biomass alone (Birch and Clark 1953) but is much more difficult to measure. Of the plant food actually assimilated by insects, some is converted to living tissue (production) and some consumed in metabolic processes (maintenance). Since our estimates of biomass showed no increase with time, we can assume that production and mortality were approximately equal, but the data afford no means of measuring either production or mortality. In fact, there seems to be no adequate method for measuring actual productivity for field studies of mixed insect species. In simpler systems where one or two species dominate the community, productivity of these species may be measured meaningfully (Odum and Smalley 1959). Except in 1956 when *Lygus lineolaris* (P. deB.) was abundant on smartweed, none of our insect populations was dominated by a species which would lend itself to estimates of mortality (and thus of productivity).

From the data presented in Table III, it appears obvious that our figures could have drastic errors, even of orders of magnitude, without affecting the conclusion that these insects contain only a small fraction of the total Strontium-90 and Cesium-137 in the system because there is such a large reservoir for these materials in the soil. The plants accumulate but a fraction of a percent of the soil content of radionuclides, and insects accumulate a fraction of the amount in the plants. Probably comparisons should be made to the concentrations in plants rather than to soil concentrations, since most of the radioactive materials in the lake bed soils are either not cycled through the biological system at all or, if so, extremely slowly. The insects might contain relatively higher concentrations in comparison to plants and soils in systems cycling radioisotopes from fallout, if these were more heavily concentrated directly on vegetation, or in aquatic situations.

Table III shows that about 0.04% of the burden of Cesium-137 carried by plants is found in the standing crop of herbivorous insects. This figure is not an adequate measure of the turnover of the isotope by insects for 2 reasons: (1) The concentration in the insects at any one time is a balance between intake and elimination. Although the concentration in insect tissues does not change with time, a continuous intake representing consumption of plants must occur in order to maintain the equilibrium. (2) The production of new insect biomass, although offset by mortality, also means additional consumption of plants. For a measure of actual turnover of Cesium-137 these 2 factors, maintenance and productivity, must be considered.

While we have no measures of productivity, some estimates concerning food consumption by the insect biomass may be made from information provided by the isotopes. The consistent level of radioactivity in insects throughout the summer suggested that concentration in insects had quite promptly come into equilibrium with concentrations in their food supply—that their daily intake was approximately balanced by their daily elimination. Although food consumption occurs at a constant rate (grams per day) elimination of isotopes occurs at a rate proportional to the body concentration. Such a balance in concentrations was found in laboratory experiments by Crossley and Pryor (1960) on *Romalea microptera,* where a high rate of biological elimination, λ, was found for Cesium-137. The total radioactivity at equilibrium, Q_e, tends to be lost at a rate λQ_e. The physical half-life of Cesium-137 is so long (about 30 years) that physical decay is of no significance and λ may be used to represent biological elimination alone. Davis and Foster (1958) showed how the steady state is maintained only by balancing the loss due to elimination by a certain rate of assimilation *ra,* where *r* is the rate of ingestion and *a* represents the proportion of the ingested material assimilated:

$$ra = \lambda Q_e \qquad (1)$$

For the grasshopper *Romalea microptera,* λ was estimated from observed rates of elimination of radioactivity and also from the rapid approach to equilibrium (Crossley and Pryor 1960). From those data a biological half-life (T_b) of about 4 days (time to eliminate 50% of the body burden) was estimated. λ is $(\ln 0.5)/T_b = 0.693/T_b = 0.17$. Biological half-lives of 2 to 3 days for Phosphorus-32 in *Drosophila* species were reported by King (1954). Still lower values of T_b, and thus higher values of λ, may be appropriate for the elimination of Cesium-137 from some of the minute insects of the lake bed fauna.

The fraction *a* which is absorbed from the ingested material is not known. While ingested cesium is almost completely absorbed from the digestive tract of mammals (Hood and Comar 1953) such complete absorption seems unlikely in the insects.

Solving equation (1) for *r* gives an approximation of the feeding rate required for maintenance of the body burdens in the insects. For Cesium-137, conservative estimates are $a = 1$ and the average $\lambda = 0.17$ ($T_b = 4$ days). The average Cesium-137 concentration for the insects listed in Figure 6 is 0.865×10^{-4} µc per g dry wt. By substituting these values in equation (1), *r* is estimated at 0.150×10^{-4} µc per g insect per day. Since the concentration in the plants listed in Figure 6 averages 1.103×10^{-4} µc per g dry wt, dividing the estimate for *r* by this figure gives 0.136 g plant consumed per g insect per day. Using the estimate of 300 mg dry wt of insects per square meter, consumption can be expressed as .0408 g plant per square meter per day. In a 100-day growing season, insects consume 4.08 g plant per square meter. Since the plant biomass averages about 600 g per square meter, consumption by insects amounts to 0.7% of the plant biomass.

This estimate of 0.7% of the plant biomass consumed by insects is based on conservative estimates of *a* and λ. Table IV presents the results of calculations similar to those given above and using varying estimates of *a* and λ. For the extreme conditions of $a = 0.25$ (only 25% of the ingested cesium is absorbed) and $\lambda = 1.39$ (a biological half-life of only 0.5 days), consumption by insects would amount to about 20% of the vegetation. However, the insects considered are of mixed species, and undoubtedly have a mixture of high and low elimination rates and fractions of absorption. For such a mixed population, the most reasonable estimates for plant consumption by insects would involve higher estimates of *a* (between 0.75 and 1.0) and a biological half-life of about 1 day ($\lambda = 0.693$); under these assumptions insect consumption of plants amounts to about 3% of the plant biomass. This much feeding is necessary for maintenance of the standing crop; actual production of insect tissue involves further plant consumption which must be added to these figures.

TABLE IV. Percentage of plant biomass consumed by herbivorous insects, as estimated with different λ and *a* for Cesium-137 (λ = elimination constant, *a* = fraction absorbed, T_b = biological half-life)

a	γ			
	0.173 (T_b=4 days)	0.346 (T_b=2 days)	0.693 (T_b=1 day)	1.39 (T_b=0.5 day)
1.0	0.7	1.4	2.7	5.5
0.75	0.9	1.9	3.6	7.4
0.50	1.4	2.8	5.4	10.9
0.25	2.7	5.4	10.9	21.8

It may be seen from Table III that the above calculations, if performed for Strontium-90, using the same λ and *a,* would produce different results than those for Cesium-137. Insect biomass contains but 0.006% of the Strontium-90 concentration in the plant biomass, as compared to 0.04% for Cesium-137. It would appear, however, that much higher estimates of λ would be required for calculations involving Strontium-90. Grosch and LaChance (1956) reported a T_b of less than 1 day ($\lambda = 0.7$) for Strontium-89 for female wasps, *Habrobracon.* Unpublished data (Crossley) indicate that strontium is eliminated far more rapidly than is cesium from grasshoppers. The discrepancy between the plant-insect ratio of the concentrations for these 2 isotopes may be due to marked differences in rates of elimination by the insects. If higher estimates of λ (shorter biological half-life) and lower estimates of *a* (less absorption) are used, food consumption estimates based on Sr^{90} are similar to those based on Cs^{137}.

There is a further reason for basing our estimates on Cesium-137 rather than Strontium-90 concentrations. The estimates of concentrations in the insects (Q_e) include the unabsorbed plant material in the insect digestive system at the time the insects were collected. This is not a serious objection in the case of Cesium-137 since insect and plant concentrations are similar; the gut contents are small compared to the body. With Strontium-90, however, insect concentrations are an order of magnitude lower than concentrations in plants; the gut contents would contribute 10 times as much activity per unit weight as the insect tissues themselves. Therefore, better estimates of plant consumption by insects are those based upon Cesium-137.

STRUCTURE OF INSECT POPULATIONS

In order to refine the estimates given in the previous section, much more detailed analyses of the insect populations are necessary. This section gives an abbreviated account of the insect populations which developed on the White Oak Lake bed vegetation. These data also are of interest in that they illustrate the successional changes in insect populations on a new area for which a known time scale is available.

In all, 401 species of insects were identified from the vegetation of White Oak Lake bed. The species list itself is too lengthy to be reproduced here, but has been published separately (Howden and Crossley, in press). A limited number of copies of the list are available from the senior author.

THE SEDGE-RUSH ASSOCIATION

1956 samples

A general picture of the insect population in the sedge-rush areas in late summer may be obtained from Table V, which shows the average numbers of insects per 10-sweep sample for the major insect groups. Since systematic sampling was not begun until August, these samples do not represent the earliest insects to appear on the vegetation. Rather, these were the populations which developed after invasion and establishment by the insect species. The center and inshore areas show good agreement in both total numbers and in dominant groups. Differences may exist between the center and inshore replicates but, if so, they are less than the differences between the vegetation types.

Grasshoppers, leafhoppers and delphacids, Hemiptera, and Diptera were most abundant (Table V). The other insect groups represented a variety of species but few individuals.

TABLE V. Mean number of insects and spiders per 10-sweep sample in 1956 (based on 6 samples taken in August-September)

Insect Group	Sedge-Rush Center	Sedge-Rush Inshore	Smartweed Center	Smartweed Inshore
Grasshoppers	13.0	8.0	5.0	7.2
Leafhoppers and Delphacids	33.8	42.3	4.0	7.3
Other Homoptera	0.3	1.3	0.3	0.0
Miridae	1.8	1.8	36.7	28.7
Other Hemiptera	24.5	15.3	10.5	8.5
Crysomelidae	3.0	3.5	1.7	1.3
Coccinellidae	7.2	5.8	5.2	5.8
Bees	0.7	0.2	5.7	11.8
Other Hymenoptera	1.7	1.2	0.3	1.3
Diptera	18.8	36.8	18.7	16.5
Lepidoptera	1.5	0.2	2.0	1.3
Spiders	3.8	5.2	3.5	6.0
Totals	110.1	121.6	94.1	95.8

Leafhoppers and delphacids, which averaged 30-40 individuals per sample, were the most abundant insects. Two species, *Graminella nigrifrons* (Forbes) and *Delphacodes puella* (Van D.), accounted for more than 60% of the leafhoppers and delphacids collected. These are common inhabitants of low, grassy areas.

Of the grasshoppers, *Conocephalus fasciatus* (De G.) and *C. brevipennis* (Scudd.) were the most numerous. These insects also have broad distributions. About 50% of the grasshoppers collected were immatures.

Numbers for the hemipteran species are given in Table VI. The predaceous lygaeid *Geocoris punctipes* (Say) was the most numerous hemipteran in the sedge-rush areas. *Cymus angustatus* Stål, a widespread species, also occurred in numbers.

TABLE VI. Numbers of insects of the order Hemiptera on vegetation (totals of 6 samples taken August-September, 1956)

Species	Sedge-Rush Center	Sedge-Rush Inshore	Smartweed Center	Smartweed Inshore
Lygus lineolaris adults	10	11	109	99
Lygus lineolaris nymphs	0	0	134	79
Arhyssus lateralis	8	6	24	17
Geocoris punctipes (predator)	75	63	13	11
Cymus angustatus	39	6	0	0
Sinea spinipes (predator)	8	7	0	0
Jalysus wickhami	0	0	1	7
Orius insidiosus (predator)	0	0	2	7
Misc. Hemiptera	15	11	11	8

The Diptera were numerous but contained such an abundance of species that they proved difficult to handle taxonomically. The most numerous of the flies were the midges (Tendipedidae), even though their numbers were underestimated by our sampling method. Members of the family Chloropidae, particularly *Thaumatomyia glabra* (Mg.), were abundant. Numbers of this species were highest in the last of August, when they were 15-20 per 10-sweep sample. The high mean of 36.8 (Diptera) per sample in the sedge-rush inshore area (Table II) was due to the collection of a swarm of 108 midges in one sample.

Thus the 1956 samples were dominated by a cicadellid, a delphacid, 2 species of grasshoppers, a predaceous lygaeid, and a mixture of fly species. These insects are found normally in low, grassy habitats. Their numbers accounted for about 80% of the insects collected.

1957 samples

Samples of insects from the sedge-rush area in 1957 revealed a smaller number of insects but a greater diversity of insect species (Tables VII and IX), as compared to the 1956 samples. The average number of insects per sample was about 60 in 1957, compared with an average of 110-120 insects per sample in 1956. The orders which were most numerous in 1956 were also most numerous in 1957, but their predominance was not so great. Again there was little if any consistent difference between center and inshore replicates.

TABLE VII. Mean number of insects and spiders per 10-sweep sample in 1957 (based on 14 samples taken June-September)

Insect Group	Sedge-Rush		Smartweed		Willow	
	Center	Inshore	Center	Inshore	Center	Inshore
Grasshoppers	3.5	4.1	3.8	7.8	5.6	5.1
Leafhoppers and Delphacids	14.0	10.9	11.4	13.9	12.2	8.5
Other Homoptera	1.6	6.4	2.4	3.4	2.4	3.3
Miridae	0.5	0.6	7.6	6.1	1.7	0.9
Other Hemiptera	6.5	5.7	11.2	8.6	1.9	0.9
Chrysomelidae	5.3	2.1	6.5	6.7	32.2	20.5
Coccinellidae	4.7	4.9	1.2	1.1	1.3	2.1
Bees	0.7	2.4	11.1	8.9	1.9	2.0
Other Hymenoptera	2.7	3.6	5.1	4.6	3.9	2.9
Diptera	15.5	10.8	18.4	13.8	11.0	12.5
Lepidoptera	2.2	5.1	1.6	2.5	2.7	2.3
Spiders	6.5	6.4	7.3	7.6	4.5	5.4
Others	0.1	0.4	0.1	0.4	0.7	0.0
Totals	63.8	63.4	87.7	85.4	78.4	70.0

Table VIII presents the average number of insects per sample taken during the last 6 weeks of the 1957 season. These data are perhaps more comparable to the 1956 collections than the data in Table VII, since the 1956 samples were taken at the end of summer only. Data for the last 6 weeks of the 1957 season bear the same general relationship to the 1956 data as do the data for the entire summer of 1957. Insofar as these broad categories are concerned, the composition of the samples showed little change during the summer of 1957. There was only a slight increase in the relative abundance of the more numerous forms. Changes did occur, however, in the species composition of these broad groupings during the summer.

TABLE VIII. Mean number of insects and spiders per 10-sweep sample taken in the last 6 weeks of 1957 (August-September)

Insect Group	Sedge-Rush		Smartweed		Willow	
	Center	Inshore	Center	Inshore	Center	Inshore
Grasshoppers	3.7	1.5	0.3	1.0	1.7	0.3
Leafhoppers and Delphacids	19.3	9.0	6.3	10.3	4.2	11.7
Other Homoptera	1.7	9.5	1.2	2.5	2.7	2.8
Miridae	0.3	0.3	3.7	3.7	0.5	0.3
Other Hemiptera	6.0	3.5	12.2	8.7	1.5	2.8
Chrysomelidae	7.2	2.8	8.7	11.7	59.7	36.0
Coccinellidae	2.3	4.7	1.8	2.3	0.8	1.1
Bees	1.5	5.2	19.7	18.3	2.8	3.7
Other Hymenoptera	4.5	4.8	4.3	3.8	4.8	3.7
Diptera	18.0	8.2	15.3	7.3	6.2	9.4
Lepidoptera	1.2	4.2	2.3	4.0	2.2	2.0
Spiders	7.3	7.5	11.8	12.0	5.0	4.3
Other	0.0	0.0	0.2	0.2	0.3	0.0
Totals	72.2	61.2	85.8	83.8	90.0	76.5

Diptera were the most abundant insects of the sedge-rush association in 1957. The diversity of species exceeded that for 1956. Chloropids and midges were the most numerous flies collected. *Thaumatomyia glabra* (Mg.), abundant during August of 1956, declined in August of 1957. *Chlorops* spp. also were numerous. *Eumetopiella rufipes* (Macq.) (Otitidae) became numerous in August.

Leafhoppers and delphacids were almost as numerous as the dipterans in the 1957 samples. *Graminella nigrifrons* (Forbes) and *Delphacodes puella* (Van D.), with an average of about 2 individuals per sample, decreased by a factor of 10 in comparison with the 1956 samples. However, the number of species found increased from about 10 in 1956 to about 50 in 1957. No species was present in large numbers.

Grasshoppers were notably less numerous in 1957 than in 1956. *Conocephalus* spp. averaged 15 per sample in June but declined to 1 per sample by late July.

Hemipterans were strikingly reduced in numbers in 1957. *Geocoris punctipes* (Say), the most numerous hemipteran in 1956, was not even collected from sedge-rush in 1957. *Cymus angustatus* Stål was the most numerous hemipteran.

These 4 insect groups, the grasshoppers, leafhoppers and delphacids, dipterans, and hemipterans, include about 50-60% of the individuals collected in sedge-rush in 1957. No single species in these groups was clearly a dominant one. All of the species present in 1956 seem to have decreased in numbers in 1957 (with the possible exception of some of the dipteran species, which could not be handled adequately, taxonomically).

1958 samples

Samples of insects in sedge-rush areas in 1958 revealed an insect community similar to that found in 1957. Dipterans, a mixture of species, were the most numerous insects collected. Leafhoppers and delphacids were second in abundance, and hemipterans were third. Less attention was paid to species identification in 1958, but the species composition of these groups seemed similar to the 1957 collections.

THE SMARTWEED ASSOCIATION

1956 samples

The general composition of the insect samples taken in August-September, 1956, is given in Table V. As in the case of the sedge-rush association, these insects are not the earliest invaders but are those which established populations. Since smartweed produces flowers attractive to insects, the differences between early season and late season collections may be more important than with the sedge-rush.

The most abundant insect groups on smartweed were the hemipterans, bees, and dipterans. These abundances were seen in both the center and inshore replicates, and agreement between the replicates seems good.

Hemipterans were clearly the most abundant insect order. Table III gives the total individuals collected for the hemipteran species. A single species, *Lygus lineolaris* (P. deB.), accounted for most (about 80%) of the hemipterans collected. This was also the most abundant of any of the insect species on smartweed. The population size reached could probably be considered as economic (in the sense of applied entomology); as many as 70 individuals were taken in a single sample. Evidently there was little damage to the smartweed, since it grew luxuriantly.

The dipterans, although numerous, were represented by many species. Midges and chloropids, particularly *Thaumatomyia glabra* (Mg.), were the most abundant of the dipterans.

Bees were conspicuous members of the smartweed community. The smartweed was in bloom when the collections were begun and the number of flowers was only beginning to decline in the last of August. Most of the bees collected were sweat-bees of the genus *Lasioglossum,* with the species *L. inconspicuum* Sm. predominating. Among others, *Apis mellifera* L. was collected but only in small numbers.

A mirid, the bees, and the dipteran species, accounted for about 70% of the insects collected from smartweed in 1956. Seemingly, all of these are normal inhabitants of smartweed.

1957 samples

Numbers of insects per sample in 1957 (Table VII) were similar to the numbers found in 1956. The number of species present on smartweed increased in 1957, and there was a corresponding decrease in population sizes for the species which were numerous in 1956.

Comparisons of the average numbers per sample during the entire summer with the averages for the last 6 weeks of the summer (Table VIII) show that changes occurred in the relative abundances of the insect groups. Actually, numbers of grasshoppers, mirids, and dipterans declined during the summer, while numbers of beetles, bees, and spiders increased. The compositions of the samples during the summer of 1957 tended to become increasingly dissimilar to the samples taken in August of 1956. Most notably, the decrease in mirids [mostly *Lygus lineolaris* (P. deB.)] is the exact opposite of the results obtained in 1956.

The most abundant insect groups on smartweed in 1957 were hemipterans (but not mirids), leafhoppers and delphacids, bees, and dipterans.

The hemipterans included a complex of species normally occurring on smartweed. *Arhyssus lateralis* (Say), *Orius insidiosus* (Say), and *Pachybrachius albocinctus* Barb., each occurred in densities of about 2-4 individuals per sample. *Lygus lineolaris* (P. deB.) occurred throughout the summer in densities of 5-6 individuals per sample.

Leafhoppers and delphacids were represented by about 25 species. *Graphocephala versuta* (Say) was seemingly the most numerous, with densities of about 4 individuals per sample.

Bees, as a group, tended to increase with time, as more blooms appeared. About 70% of the individuals collected were *Lasioglossum inconspicuum* Sm. Most of the other species were in scattered collections but the totals tended to increase in August.

Diptera were represented by an abundance of species, with the midges being the most numerous.

Thaumatomyia glabra (Mg.) (Chloropidae) was also numerous.

1958 samples

By the summer of 1958, smartweed had become too diffuse to sample on most of White Oak Lake bed. A rather small band of smartweed extended along the creek, however, and this was sampled as the "center" replicate. No "inshore" samples were taken. The total number of insects per sample showed some reduction in 1958, as compared to 1956 and 1957. Almost every group showed some reduction in numbers. The only notable increase in numbers was in the Coleoptera, and this was due to the flea beetle *Systena frontalis* (Fabr.) which occurred in numbers of 14-31 per sample in July and August.

Second in abundance to the Coleoptera were the Diptera, which averaged 11 insects per sample. The other groups all averaged less than 10 insects per sample.

The Willow Association

1956 samples

None were taken, since the willows were not numerous or large enough to be considered a major plant association on the lake bed.

1957 samples

Table VII gives the numbers of insects per 10-sweep sample for the major insect groups on willow. The beetles, leafhoppers and delphacids, and dipterans were particularly abundant.

The beetles included a variety of species but most of the individuals belonged to the flea beetle species, *Chalcoides fulvicornis* (Fabr.). This species averaged about 5-10 individuals per sample in June but increased to about 50 per sample in August. It was by far the most abundant species in samples from willow. Figure 7 shows the numbers of *Chalcoides* per 10-sweep sample by weeks. The large increase in the latter part of the summer is seemingly due to the appearance of a 2nd generation of adults.

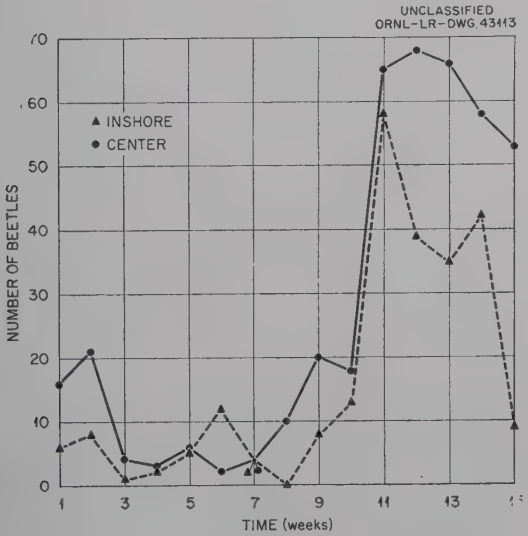

Fig. 7. Number of willow flea beetles per sample: Summer 1957.

Leafhoppers and delphacids were represented by a number of species, but none of them was particularly abundant. Many of the leafhopper species collected in the sedge-rush and smartweed areas were taken on willow also. Dipterans, as well, included a variety of species.

1958 samples

By 1958, willows on the lake bed had grown to such a size (10-15 ft) that it is doubtful whether the 10-sweep method of sampling had any relationship to an area basis. The extent of the willow stands on the lake bed increased also.

The same broad insect groups were abundant in 1958 as in 1957. These were beetles, leafhoppers and delphacids, and dipterans.

The flea beetle, *Chalcoides fulvicornis* (Fabr.), with numbers of 80-80 per sample, was by far the most abundant insect. These samples show a marked increase over the 1957 counts. However, the biggest collections were made at the beginning of the summer, rather than at the end as in 1957.

Discussion of Insect Populations

Once established, the 3 vegetation types sampled continued to change with respect to their abundances on the lake bed during the course of the study. Willows increased in extent of coverage, the sedge-rush association remained at about the same amount of coverage, and the smartweed association decreased. Certain parallels may be drawn between these changes and changes in the insect populations in these vegetation types.

In each of the vegetation types, the first year's collections of insects showed comparatively few species represented by many individuals. The composition of the samples during the following years seemed to be related to the change in coverage of the particular vegetation type, as well as to the increasing heterogeneity of the originally rather pure stands.

The insects on willow had similar abundance and species composition in 1957 and 1958. Species which were clearly dominant in 1957 maintained their dominance in 1958. In contrast, the insects on the sedge-rush and smartweed in the 2nd year showed a decrease in numbers of individuals and an increase in numbers of species (see Tables V and VII). The greatest decrease in population size occurred in the 2nd year (1957) in the sedge-rush areas and in the 3rd year (1958) in the smartweed areas. However, in both of these vegetation types the insects dominant in 1956 were sharply decreased in numbers in 1957.

Evidently, the insect faunas characteristic of the sedge-rush and smartweed vegetation types required 2 or more seasons to reach maximum number of species, with the greatest change in composition occurring between the first and 2nd seasons. Since the willows were extending their coverage, the expanded habitat each season may be responsible for the continued high populations of the dominant species, since pure new stands were available for exploitation each year. An additional factor was the increase in abundance of plants such as *Solidago* and *Eupatorium* in the sedge-rush and smartweed areas, which provided additional insect habitats.

The proximity of other similar communities might also be important in insect invasion of a newly-established plant community, since insect species differ in their capacities for dispersal. However, the vagilities of insect species seem to be of minor importance in the present study. Prior to drainage, the margins of White Oak Lake supported many plant species which subsequently migrated onto the drained lake bed. Certainly the sedge-rush and willow species occurred there. Smartweed was growing among the mixed forbs on the margins of White Oak Lake. Thus the insects characteristic of these plant types could have been in the immediate vicinity of the drained lake bed when plant invasion started.

That some significant change in species composition occurred between years may be seen in Table IX. Here the numbers of insect species in 1956 and 1957 are compared for the sedge-rush and smartweed populations. The insects which were present in both 1956 and 1957 constituted only about half of the total numbers of species collected, the others being present only in 1956 or in 1957. (Comparisons were made for late summer collections only, since no early summer collections were taken in 1956). The species which first appeared in 1957 constitute high percentages of the total for the Orders Homoptera, Coleoptera, and Hymenoptera. Data for 1958 are not sufficient for such comparisons but those samples did not reveal so many species new to the area as 1957.

TABLE IX. Comparison of numbers of late summer insect species on White Oak Lake bed (sedge-rush and smartweed areas only)

Insect Order	Species Found Only in 1956	Species Found in Both Years	Species Found Only in 1957	Total
Orthoptera..........	5	7	3	15
Hemiptera..........	5	13	7	25
Homoptera..........	3	7	24	34
Coleoptera..........	4	26	15	45
Hymenoptera........	10	21	33	64
Diptera.............	18	22	23	63
Totals..........	45	96	105	246
Total for each year	141		201	

The insect populations seemed to be typical for the plants involved. No evidence of unusual host relationships was found, nor does it appear that any species normally abundant on these host plants in this area was absent from the lake bed associations. The unusual numbers of some species [*Lygus lineolaris* (P. deB.) in 1956, *Systena* spp. in 1957] might have been caused by any of a number of environmental variables not measured in this study. In general, the insect populations showed no conspicuous abnormalities during or after the first 2 seasons.

SUMMARY

The development of insect populations on vegetation growing on White Oak Lake bed was followed for 3 years (1956-1958), immediately following the draining of White Oak Lake. This lake had served as a final holding basin for Oak Ridge National Laboratory's low-level wastes, and the alluvial terrain exposed upon drainage contained significant concentrations of radioisotopes, including Strontium-90 and Cesium-137.

The insect biomass, estimated by sweep-net and box-trap methods, was about 200-300 mg/m^2. No change could be demonstrated during the seasons, and evidently little change occurred between years.

Significant concentrations of both Strontium-90 and Cesium-137 were found in samples of herbivorous insects. Concentrations of Strontium-90 were about 25% of the soil values, and Cesium-137 concentrations were about 1% of the soil values. However, the biomass of insects was minute compared to plant and soil masses, and the herbivorous insects contained but a minute fraction of the fission products in the system, since the bulk of these radioisotopes are in the soil. A sizeable fraction of the materials taken up by plants, however, may pass through the herbivorous insects in the system.

Insect populations were followed in 2 areas each of smartweed, sedge-rush, and willow vegetation. Each of the vegetation types acquired its own characteristic insects. First-year insect populations tended to be dominated by one or a few species represented by many individuals. The second-year populations showed a reduction in numbers for the dominant species and an influx of additional species, accompanying an increase in plant diversity. No such reduction of the dominant species occurred in the willow areas, presumably because the willows were increasing their coverage each year, and additional species of plants were not invading the willow stands.

ACKNOWLEDGMENTS

We gratefully acknowledge the contributions of our colleagues to this study. For aid and advice, both in field and laboratory, we thank Doctor S. I. Auerbach and Mr. Paul B. Dunaway, Oak Ridge National Laboratory. Certain plant and soil data were provided by Dr. Auerbach and by Doctors Royal E. Shanks and H. R. DeSelm, University of Tennessee. We were fortunate in having as assistants Mr. Madison E. Pryor and Mrs. Jane H. Marks, both formerly of Oak Ridge National Laboratory. Doctors Jerry S. Olson, Oak Ridge National Laboratory, Royal E Shanks and H. R. DeSelm, University of Tennessee, and Eugene P. Odum, University of Georgia, kindly criticized the manuscript.

The following specialists made identifications of the insect species: ORTHOPTERA: T. H. Hubbell, University of Michigan. HOMOPTERA: J. P. Kramer, L. M. Russell, K. Sommerman, USNM, and David A. Young, North Carolina State Coll. HEMIPTERA: R. I. Sailer, USNM. ZYGOPTERA: S. Parfin, USNM. DIPTERA: C. W. Sabrosky, Alan Stone, R. H. Foote, W .W. Wirth, USNM. HYMENOPTERA: B. D. Burks, K. V. Krombein, C. F. W. Musebeck, M. R. Smith, L. M. Walkley, USNM, H. Townes, University of Michigan, and T. B. Mitchell, North Carolina State Coll. LEPIDOPTERA: J. F. Gates Clark, E. L. Todd, USNM. COLEOPTERA: H. F. Howden, Entomology Research Institute, Ottawa.

To these persons, and to others who contributed, we extend our thanks.

REFERENCES

Auerbach, S. I. 1959. Ecological Research: White Oak Lake bed studies. Health Physics Division Annual Progress Report for Period Ending July 31, 1959. ORNL-2806, Health and Safety, TID-4500.

Birch, L. C. and D. P. Clark. 1953. Forest soil as an ecological community. Quat. Rev. Biol. **28**: 13-36.

Cross, W. H. 1956. The arthropod component of old field ecosystems: Herb stratum populations with special emphasis on the Orthoptera. Doctoral Dissertation, Univ. Georgia.

Crossley, D. A., Jr., and M. E. Pryor. 1960. The uptake and elimination of Cesium-137 by a grasshopper—*Romalea microptera.* Health Physics **4**: 16-20.

Davis, J. J. and R. F. Foster. 1958. Bioaccumulation of radioisotopes through aquatic food chains. Ecology **39**: 530-535.

Grosch, D. S. and L. E. LaChance. 1956. The fate of radiostrontium fed to Habrobracon females. Science **123**: 141-142.

Hassett, C. C. and D. W. Jenkins. 1952. Use of fission products for insect control. Nucleonics **10**: 42-46.

Howden, H. F. 1957. Investigations on sterility and deformities of *Onthophagus* (Coleoptera, Scarabaeidae) induced by gamma radiation. Ann. Ent. Soc. America **50**: 1-9.

Howden, H. F. and S. I. Auerbach. 1958. Some effects of gamma radiation on *Trogoderma sternale* Jayne. Ann. Ent. Soc. America **51**: 48-51.

Hoffmann, C. H., H. K. Townes, H. H. Swift, and R. I. Sailer. 1949. Field studies on the effectiveness of airplane applications of DDT on forest invertebrates. Ecol. Monogr. **19**: 1-46.

Hood, S. L. and C. L. Comar. 1953. Metabolism of Cesium-137 in rats and farm animals. Arch. Biochem. and Biophys. **45**: 423-433.

King, R. C. 1954. Studies on radiophosphorus in Drosophila. II. The turnover and distribution of phosphorus in adult Drosophila. J. Exp. Zool. **125**: 331-352.

Lee, P. K. and S. I. Auerbach. 1958. Determination and evaluation of the radiation field above White Oak Lake bed. ORNL-2755 (Oak Ridge National Laboratory).

Odum, E. P. and A. E. Smalley. 1959. Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in a salt marsh ecosystem. Proc. N. A. S. **45**: 617-622.

Shanks, R. E. and H. R. DeSelm. 1956. Plant taxa occurring on White Oak Lake bottom following drainage. (Unpublished list.)

Wolcott, G. N. 1937. An animal census of two pastures and a meadow in northern New York. Ecol. Mono. **7**: 1-90.

GROWTH AND REPRODUCTION OF THE OYSTER DRILL *EUPLEURA CAUDATA* IN THE YORK RIVER, VIRGINIA[1]

CLYDE L. MACKENZIE, JR.[2]
Virginia Fisheries Laboratory, Gloucester Point, Virginia

INTRODUCTION

Eupleura caudata (Say) (Order Neogastropoda: Family Muricidae), the thick-lipped or rough oyster drill, is a close relative of the smooth drill, *Urosalpinx cinerea,* which occurs within the same geographical range along the shores of the Atlantic coast from Massachusetts to the eastern coast of Florida. Both species are well-known predators of oysters and perhaps other commercially valuable bivalves. Except in isolated localities, *U. cinerea* is the dominant species and as a result has received more scientific study. Until Haskin (1935) showed that *E. caudata* females deposit more embryos per case than *U. cinerea* in Barnegat Bay, New Jersey, and noted the differently-shaped cases, the only publicized difference between the 2 species lay in morphology of the shell. Though the species is present in some numbers on the bottom, McHugh (1956) did not find a single *E. caudata* among hundreds of drills collected from pier pilings in the vicinity of Gloucester Point, and we found only 3 in our samples of several hundred drills collected from pier pilings in this area. This indicates that the 2 species have different vertical distributions. Haskin (1935) and Galtsoff, Prytherch and Engle (1937) state that the species do not differ in their destructiveness of oysters. Stauber (1943) observed copulation by a single pair and he states that numbers of embryo cases deposited by caged females vary from year to year. Engle (1935) and Andrews (1955) briefly describe spawning patterns for a single year. Other than the fact that certain workers believe the ratio of *E. caudata* to *U. cinerea* is increasing in some localities, little is known about the natural history of this animal (Carriker 1955).

---

[1] This research was conducted under a contract with the U. S. Fish and Wildlife Service, No. 14-19-008-2372, Study of Oyster Drills in Chesapeake Bay.

[2] Present address, U. S. Fish and Wildlife Service, Biological Laboratory, Milford, Connecticut.

This study was undertaken to elucidate certain aspects of growth, reproduction, and ecology of *E. caudata* in the eelgrass zone of the York River, Virginia, to acquire basic information which might be used in controlling this pest.

This paper is part of a thesis submitted to the College of William and Mary in partial fulfillment of the requirements for the degree of Master of Arts. The writer wishes to express his deep appreciation to Dr. William J. Hargis, Jr. for suggesting the problem and for his valuable advice and criticism throughout this study. Thanks to Mr. Robert S. Bailey for taking the photographs, to Dr. J. L. McHugh for helping with the writing, and to many other people for their assistance. Drs. Jay D. Andrews and Melbourne R. Carriker, and Messrs. James B. Engle, John B. Glude, and W. A. VanEngel have generously given their time to reviewing the manuscript.

MATERIALS AND METHODS

Description of the area

All drills studied were taken in the vicinity of the Virginia Fisheries Laboratory at Gloucester Point, Virginia, 6 miles from the mouth of the York River (Figure 1). This area is estuarine, salinities varying between 14 and 22 $^0/_{00}$ except during severe droughts and freshets. Oyster drills and several other snails live within the eelgrass *Zostera marina* zone, a strip about 50 yards wide in the experimental area bounded by Marshall's Pier and the ferry pier. The grass is dense and almost continuous. At extreme low tides the inner edge of the zone of grass is exposed and, because the bottom slopes moderately away from shore, the outer edge is rarely covered by more than 5 or 6 feet of water. The experimental area, behind the tip of Gloucester Point, does not have rapid currents. Wave action is usually light. Within this zone, *E. caudata* had a mean density of 3 per square yard; and *U. cinerea* had a mean density of 37 per square yard, as determined by careful examination of material removed from known areas of bottom. There is little likelihood that drills migrated into or out of the experimental area because drill traps (see discussion below) placed under piers on either side or offshore of it where there was no eelgrass collected virtually no drills. Several samples of embryo cases were obtained at Tillage's oyster ground located upriver from the laboratory (Fig. 1). Except where noted, samples were taken from the experimental area.

Aquaria

Running-water aquaria of approximately 2.7 ft^3 capacity were employed to make close observations of copulation. River water from the end of the laboratory pier was continuously supplied through lead pipes by centrifugal pumps.

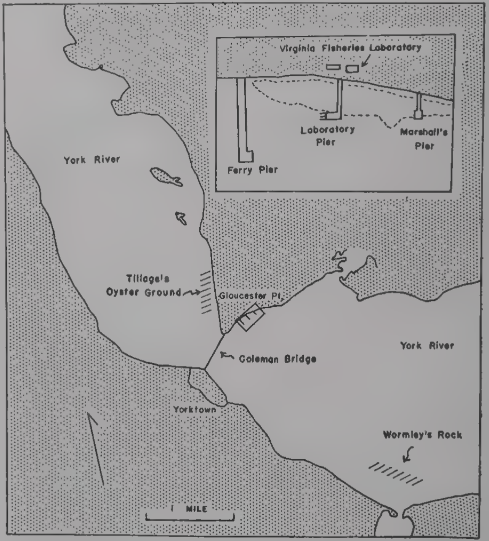

FIG. 1. York River in vicinity of the Virginia Fisheries Laboratory showing collecting sites. Inset shows experimental area. Dashed line shows extent of eelgrass.

Cages

Several phases of this study were conducted in cages, suspended along the laboratory pier one foot above bottom with about one to 3 feet of water covering them (Figures 2 and 3). Cages consisted of wooden frames with masonite bottoms. The sides and removable top were covered with large-mesh plastic screen, 4 holes per linear inch. Masonite dividers prevented contact between drills in adjacent compartments.

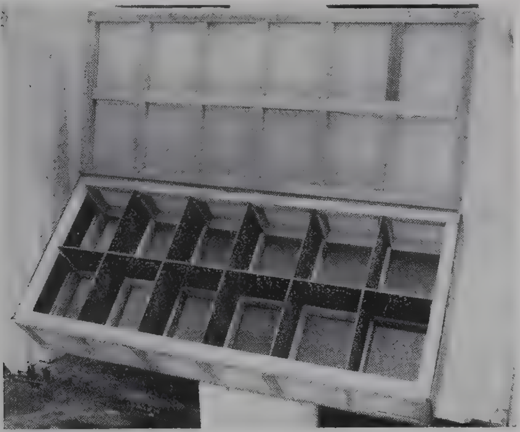

FIG. 2. Experimental cage with its screen bottom and compartments.

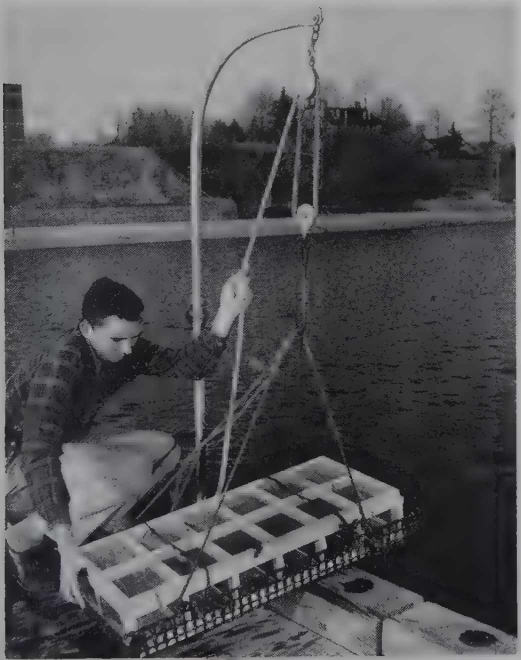

FIG. 3. Experimental cage, oyster tray, and davit used to raise and lower cage.

The cages, 37 inches long, 16 inches wide, and 6 inches deep, contained from 2 to 12 compartments each. Later models incorporated plastic screen bottoms (8 holes/inch) which permitted sediments to pass through. For support and stability, cages were placed in seasoned, tarred oyster trays similar to those used by Hewatt and Andrews (1955). Except where noted, several one- and two-year-old oysters were placed in each compartment as food and were not replaced the whole summer unless they were completely consumed by drills.

Traps

Drills and many embryo cases were obtained with traps consisting of flat, 27 × 12 inch chicken-wire bags containing small oysters and often barnacles and mussels as bait. To minimize tipping of traps upon lifting, which tends to shake out drills, traps were tied in the center of the flat side by a rope attached to a small buoy. Drills that moved to the bait were collected by carefully lifting the traps and shaking them into a shallow screen tray. Since there was a possibility that they reduced the abundance of drills locally, traps were moved to new areas after each collection to secure as many drills as possible.

Temperature

Temperature records were compiled from data collected at the U. S. Coast and Geodetic Survey tide station located at the end of the laboratory pier. Since cages and traps were 5 or more yards inshore of the temperature recorder and in shallower water, temperatures at cage and trap sites may have been slightly different from those at the tide station.

Determination of sex

The method developed by Hargis (1957) to determine sex of living snails was used. He found that oyster drills held under water would attach to one's finger. By carefully rolling the shell back the presence or absence of a penis can be detected.

Measurements

Measurements of drills made with vernier calipers and cited in millimeters are of the long axis of the shell from apical tip to siphonal tip, usually termed shell height. Cases and embryos were measured microscopically using a calibrated ocular micrometer.

GROWTH

Pattern of growth

After the initial varix (raised ridge on outside surface of univalve shell parallel to the lip) has formed when the drill is 10 to 15 mm in height,

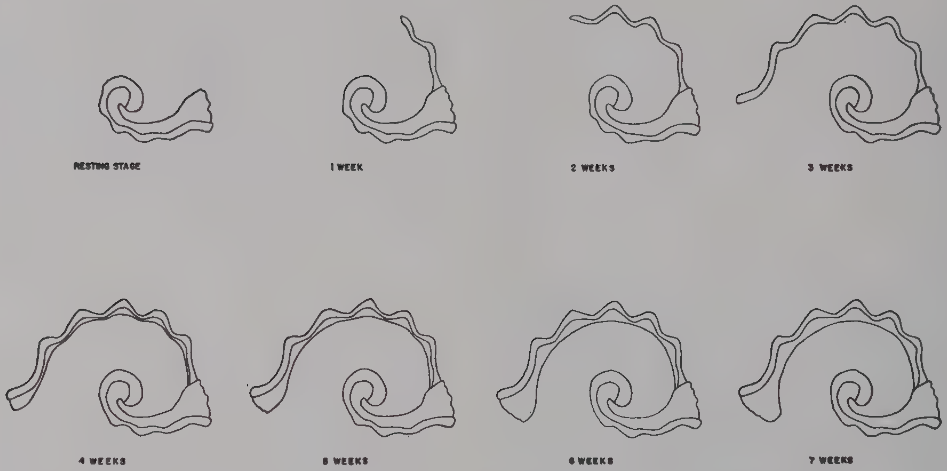

FIG. 4. Cross section of *E. caudata* shell showing pattern and approximate rate of growth. Some drills produce a flange of shell at each axial rib, not like rounded ribs as those in figure. Weeks 1-3 are termed thin-lip stages; weeks 4-7, thick-lip stages.

shell growth in *E. caudata* usually occurs as a thin layer which begins at the inner edge of the varix and without stopping to reinforce proceeds through an arc of 180°. After flaring out to form the next varix, the animal then reinforces this thin shell by depositing successive layers of shell on the inside (Figure 4). Thus thin lips are usually an indication of active growth. With the formation of each half whorl of new shell, a growth ridge, a line of demarcation between the old siphonal canal tip and the new shell, appears on the siphonal canal, and the old mark is grown over (Figure 5). During winter the thin shell covering the tip of siphonal canals of mature drills is often broken or eroded. During summer drills deposit enough new shell to cover the siphon but, unless accompanied by lateral growth, this is merely repair of shell damage and not actual growth. Moore (1936) and Hancock (1959) have shown that *Purpura lapillus* (= *Thais lapillus*) and U. *cinerea*, respectively, both prosobranch muricids, also produce a thin layer of shell which they subsequently reinforce.

Most drills from the experimental area showed a light yellowish outer layer and purplish reinforcing layers. In *E. caudata etterae* B. B. Baker (the large ecological form of *E. caudata*) from Chincoteague Bay, Virginia, however, both layers were light.

Interpretation of the growth mark

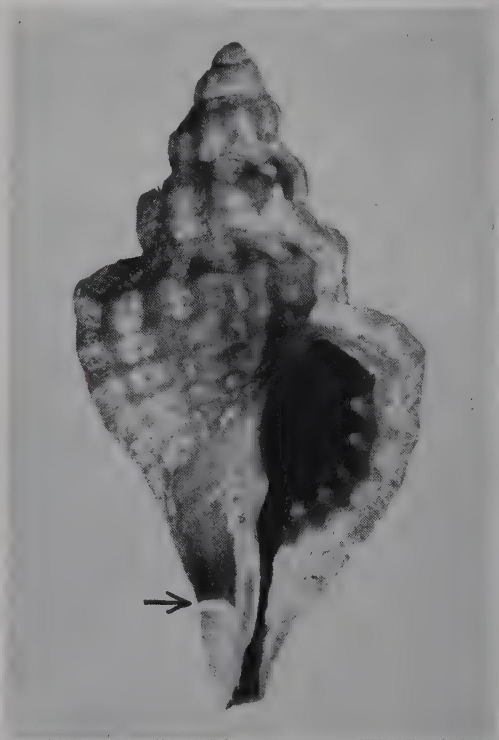

FIG. 5. Shell of *E. caudata* showing its conspicuous siphonal growth ridge.

Growth ridges or rings in many bivalves have been shown to be deposited once a year. No attempt will be made here to review all the species studied, but growth rings are year marks in the Pismo clam (Weymouth 1923), in the Pacific razor clam (Weymouth, McMillin and Holmes 1925), and in the Pacific cockle (Weymouth and Thompson 1931). To the writer's knowledge only Magalhaes (1948), who found that from none to 3 growth ridges a year with no apparent relationship to age are deposited on shells of *Busycon canaliculatum* and *B. carica,* and Clarke (1956), who without experimental evidence states that ridges on shells of *Nassarius trivittatus* are probably useless for determining age, have treated this subject with reference to snails. Cole (1942) assumed that siphonal canal ridges in British *U. cinerea* represent yearly markings and attempted to use them to determine age of drills. Andrews (1956), however, has questioned the validity of these ridges in *U. cinerea* as year marks.

The distance from growth ridges to the siphonal tip in *E. caudata* may range from 2 to 6 mm. If a year class (see below, *Recognition of year classes*) of drills large enough to have growth ridges grew more than this during a summer, many individuals would show more than one half whorl and coincident varices and growth ridges.

In May, 1956, drills with a varix ranging in height from 12.8 to 26.2 mm were caged and measured individually once a month until fall, 1957, through 2 summers and a winter. Since growth of *E. caudata* ceases at sexual maturity (see below), mature drills did not grow either summer. It was discovered that growing drills did not deposit a consistent number of half whorls. Eight of them each deposited 2 half whorls in one summer. This amount of growth appears to be normal because many drills collected in the experimental area showed 2 half whorls of shell that looked new, and several marked drills in other cage experiments deposited 2 half whorls in a summer. Seventeen drills deposited one whorl in a summer, but only 2 of these showed growth in both summers. Thus, varices and siphonal canal growth ridges in this species cannot be considered as yearly markings and appear to have little value for aging. They are merely growth stoppage marks.

Rate of shell growth

Rate of deposition of half whorls and reinforcement of them were estimated by examination of caged drills at 2-week intervals. Half whorls were deposited in 3 weeks, on the average, and reinforced in 4 weeks (Figure 4). Because the amount of food was not carefully controlled, these rates should be considered approximate. Food in the form of seed oysters was always available to drills, but their number and size, particularly, were not kept constant.

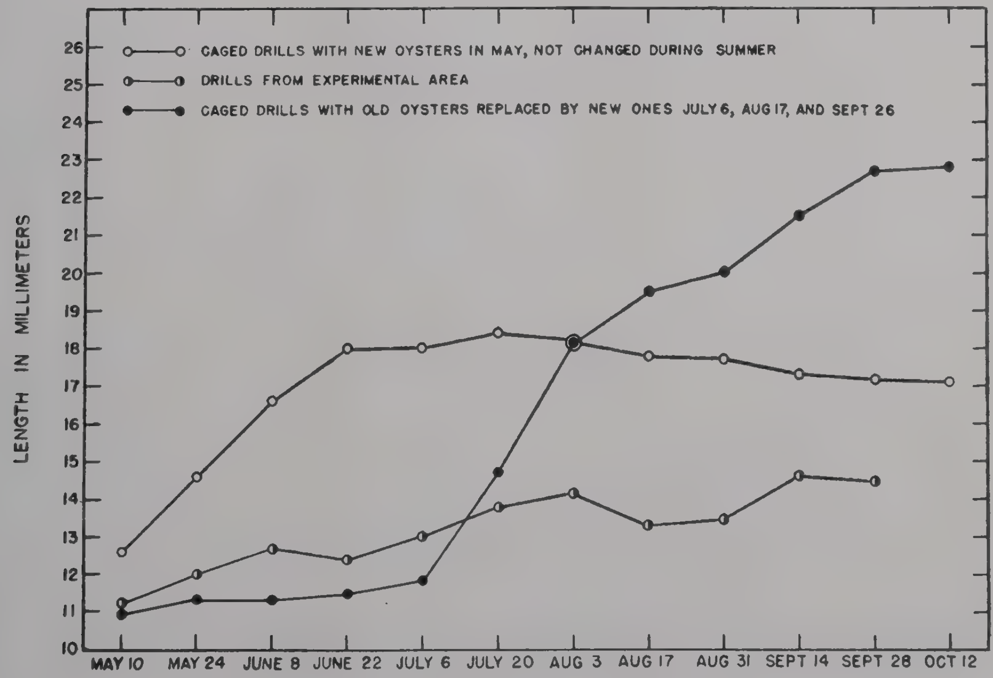

Fig. 6. Growth rates of age-group I *E. caudata* with three different food situations, summer 1957.

Growth on different amounts of food

To determine whether amount of food influences rate of growth, 3 lots of *E. caudata* of age-group I, each feeding on different amounts of food, were compared in 1957 (Figure 6). In the first lot, 64 drills were caged together on May 10 with old oysters which the drills did not bore. By July 20, all but 28 drills were dead and growth from May 10 to July 6 was negligible. On July 6, August 17, and September 26, new seed oysters encrusted with barnacles and mussels were placed in the cage. After July 6, growth was immediate and rapid and no more drills died after July 20. The 28 remaining had doubled their length by the end of September.

In the 2nd lot a pair of drills was placed in each of 12 compartments of a cage, which contained a cluster of new seed oysters with barnacles and mussels which were not changed during the entire summer. Growth was rapid until June 22 when the original heights had increased by almost one half. After this date, probably because the desirable foods had been consumed, growth ceased for the rest of the summer. Average heights actually diminished by erosion of the siphonal tip by handling.

In the 3rd lot, mean heights of drills of age-group I collected from the experimental area were determined each 2 weeks. Growth was slow as mean heights of drills increased from 11.3 to just 14.5 mm from May to the end of September.

These results suggest that amount of food has great influence on rate of growth of *E. caudata,* and that food supply is an important consideration in experimental work. With ample food, drills appear to grow much faster than they do in nature.

Cessation of growth at sexual maturity

Moore (1936, 1938) stated that *T. lapillus* ceases growth at sexual maturity. If onset of maturity in females is defined as the time when they are capable of depositing their first embryo cases and in males as the functional ability to copulate, the following data indicate a similar pattern of growth for *E. caudata.*

Beginning on June 25, 1957, a record was kept of numbers of drills in trap catches which showed evidence of recent growth, *i.e.* thin marginal lips. Though 185 of 1,108 (16.7%) age-group I drills showed thin lips, only 2 of 522 (0.4%) age-group II+ drills showed them.

In 1956 only one of 10 caged females which deposited embryo cases showed evidence of growth and that individual deposited only a half whorl of new shell. Of the 10, eight survived the winter and none grew in 1957. Of 17 other females isolated in 1956, twelve deposited cases for the first time in 1957, and did not grow during the summer. Three of the 5 reproductively-inactive in 1957 showed no growth, while one grew 2 half whorls and the other, one half whorl. It thus appears that females show little or no shell growth after embryo case deposition begins.

In 1956 only 10 of 30 caged males (height range 14.4 to 23.3 mm) grew; one of these grew 2 half whorls and 9 grew one half whorl. Since the heights range of the 30 matches that of mature copulating males, presumably most of these males were mature (Table I). Of 24 of the same males carried through 1957, 22 showed no growth and 2 grew a half whorl.

Table I. Height frequencies of copulating drills

Total height (mm)	Pairs in Aquaria 1956		Pairs in Cages 1956		Pairs and Trios in Cages 1957	
	♀	♂	♀	♂	♀	♂
14.5.....	—	1	—	—	—	—
15.5.....	—	1	—	—	—	—
16.5.....	1	2	—	1	—	1
17.5.....	0	5	—	5	—	5
18.5.....	0	4	—	10	—	8
19.5.....	2	3	—	2	—	10
20.5.....	1	0	6	11	—	6
21.5.....	3	3	6	10	1	4
22.5.....	6	7	7	5	3	1
23.5.....	2	2	10	—	20	6
24.5.....	4	—	12	—	5	1
25.5.....	1	—	2	—	5	—
26.5.....	3	—	1	—	3	—
27.5.....	2	—	—	—	2	—
28.5.....	2	—	—	—	—	—
29.5.....	1	—	—	—	—	—
30.5.....	1	—	—	—	—	—

Another indication that growth ceases when drills reach maturity is that the right limb of the height-frequency-distribution curve representing age-group II+ does not shift to the right through the growing season (Figure 7).

Recognition of year classes

Estimation of age by height frequencies

From July to November 1956 and from May to October 1957, heights of drills taken in monthly trap catches were recorded, grouped into one-mm intervals, and plotted as percentage frequency polygons (Fig. 7). In July 1956, height frequencies showed what appeared to be a single modal group. This mode showed a definite progression to the right with each successive month of 1956, and is clearly represented as the large portion of the right-hand modal group each month in 1957.

In late August 1956, five small drills appeared in trap catches and a few more were collected in

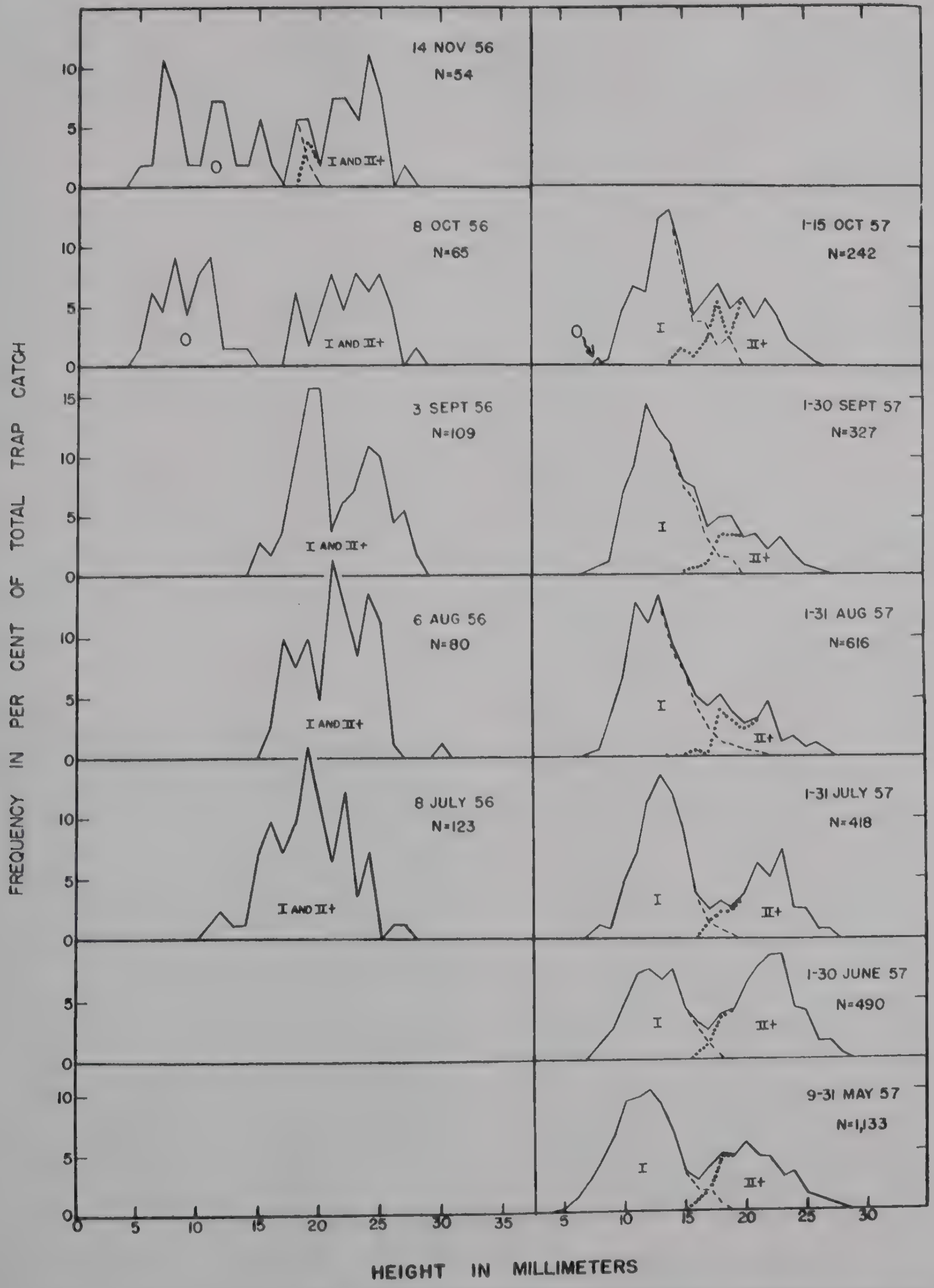

FIG. 7. Monthly trap catches of *E. caudata* in experimental area showing height frequencies of age groups O, I and II+. (The plus sign indicates age-group II and older).

September. Of 43 collected in October, a random group of 32 was measured and plotted along with the rest of the catch. This modal group with a range of 5 to 14 mm was separated by more than 3 mm from older drills. In the November 1956 sample, and in monthly samples of 1957, the left mode corresponds with the left mode of the October 1956 sample.

It is probable that drills in the left modal group in the October 1956 sample belong to age-group O. There are only 5 mm to the left of it in which to include a younger age group and separate the 2 groups by more than 3 mm. It would be unusual for age-group O to be less widely separated from the I's than the I's are from the II+'s. When first collected in late August, these drills were quite large, but in earlier observations of *U. cinerea* by Dr. J. L. McHugh (personal communication), suspected young-of-the-year drills had reached a mean size of 6 to 8 mm when they were first collected in August and September. Apparently young-of-the-year drills are not available to traps until mid-summer. Growth rate of age-group O *E. caudata* on natural bottom is unknown, but conceivably may equal or exceed that of older drills which grew from 12 or 15 mm to over 20 mm in 4 or 5 months in cages. Most *E. caudata* conchs emerged from cases during the first week of July at a height of 0.9 mm. Thus, in 3 months they had grown 5 to 10 mm.

The right modal group of the October 1956 sample probably represents age-group I and older drills. *E. caudata* ceases growth at maturity and, therefore, modal height groups coalesce. Growth of age-group I drills in 1957, as indicated by progression of the modal group about 3 mm to the right, is believed slower than in the previous year because lower height limits of the early 1956 samples were much farther to the right than those of the 1957 samples. In 1957, drills of age-group I grew much faster in cages than on natural bottom (Fig. 6). Slow growth on natural bottom may have been the result of intensive competition following a large spawning in 1956 and subsequent overcrowding of the environment. It is striking that age-group I drills are dominant in the catch in 1957. Such dominance of a year class, if it does lead to intensive competition, may subsequently affect other phases of the drill's life history, such as size of succeeding broods and age at sexual maturity.

In 1957, on October 3, only one recognizable individual (8.0 mm) of age-group O was taken. This apparent lack of young-of-the-year drills may have been the result of limited spawning and hand removal of a large percentage of the embryo cases from the experimental area.

Hancock (1959), in England, found that sizes of laboratory raised *U. cinerea* of known age fell within modal size groups of drills from nature which, because of their size relative to other drills and time of appearance in collections were suspected to be of a particular age.

Estimation of age by shell characters

Since large old-appearing shells are well-worn, it is apparent that shells of *E. caudata* erode gradually. From this, it was decided to test the hypothesis that drills could be sorted into age groups on the basis of the degree of shell erosion. *E. caudata* is perhaps an ideal gastropod to be aged by this method because the young hatch out in a period lasting only about 7 weeks, hence distinct differences in degree of shell erosion between age groups might be expected. Presumed age-group O drills of the October 1956 sample were smaller than those caught in earlier catches, and also differed in that the protoconch shell was entire and the axial and transverse ribs were sharply sculptured and not noticeably eroded. Part, or sometimes all, of the protoconch shell eroded away during the winter of 1956-57, but these drills, now called age-group I, could still be separated from older *E. caudata* because the sharp apex of the spire and the sharply-chiseled appearance of the shell sculpture had not appreciably changed. Older

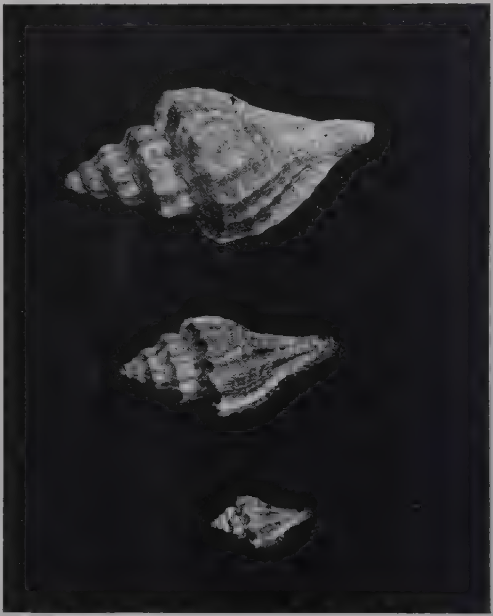

FIG. 8. Drills of age-groups O, I and II+. Axial ribs noticeable on second whorl (first whorl is apical whorl) in O specimen, on third whorl in I specimen, and on fourth whorl in II+ specimen.

TABLE II. Accuracy of observers in separating age groups, using defined morphological characteristics

Observer	AGE GROUP I					AGE GROUP II+		
	Original number	Agreement	Disagreement*	Uncertain	% Agreement	Original number	Agreement	% Agreement
A	109	109	0	0	100	32	32	100
B	109	108	1	0	99.1	32	32	100
C	109	108	1	0	99.1	32	32	100
D	108	106	0	2	98.2	32	32	100
E	108	108	0	0	100	32	32	100

* Called age-group II+.

drills, labeled age-group II+, had blunt spires and smooth ribs.

A summary of characters used to separate age-groups I and II+ on August 23, 1957, and age-group O on October 3, 1957, (Figure 8) follows:

Age-group O—Apex of spire sharp, protoconch shell entire, no noticeable erosion of shell, size small;

Age-group I—Apex of spire sharp, remnant of protoconch shell usually present, apical whorl less than 1 mm in width, axial ribs usually sharply sculptured, size moderate;

Age-group II+—Apex of spire blunt, apical whorl 1 mm or greater in width, axial ribs blunt or sharp only on last half whorl, size large.

To test reproducibility of these shell characters several laboratory staff members were asked to separate a mixed sample of age-groups I and II+. The sample had been sorted previously into groups and ages marked by inserting labeled pieces of paper into the shell cavities. Characters used to separate the groups were carefully described to the experimenters, and sample drills were furnished. In each test, drills were sorted with almost 100% agreement (Table II).

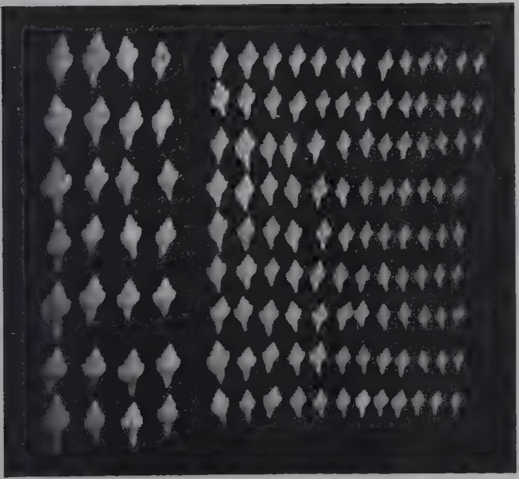

FIG. 9. Complete random trap catch (August 23, 1957) of *E. caudata* sorted by shell characters into age groups, II+ on left and I on right.

Figure 9 shows the complete catch of August 23, 1957, grouped by shell characters into age-groups I and II+.

Ages determined from height-frequency distributions and shell characters

When *E. caudata* in October and November 1956 trap catches were separated by shell characters, the height-frequency distributions of age-group O drills corresponded almost exactly with the left-hand modal group in the height-frequency polygon, and combined age-groups I and II+ drills corresponded with the right-hand modal group. In all 1957 samples, correspondence was equally close.

In May and June of 1958, these same year classes, now age-groups II and III+, could still be distinguished from each other on the basis of both height-frequency distributions and shell characters. No recognizable age-group I drills were seen.

Although much of this evidence is circumstantial and does not absolutely establish ages of individuals, shell characters are probably reliable indicators of age for most drills in a sample.

To determine age in other areas where rate of shell erosion probably differs, it may be necessary to identify the current year class late in summer and then follow it and succeeding year classes for several years. Rate of erosion could be determined by preserving shells obtained by regular sampling of a particular year class. The samples could be compared with drills of unknown age. I feel that year classes can be identified on the basis of shell characters alone after growth stops at sexual maturity when age cannot be estimated on the basis of height.

REPRODUCTION

Age and height at sexual maturity

I early suspected that female drills did not mature until after their 2nd summer of life, because in 1956, of 30 females in cages, only 11 large ones deposited embryo cases. Young-of-the-year were not yet hatched when the drills were caged, thus many of the 19 remaining were undoubtedly in their 2nd summer or age-group I. Sixteen of the 19 non-spawning females in cages survived the winter of 1956-57 and 10 deposited embryo cases in 1957. In another experiment, 9 pairs of age-group I drills (range 7.1-17.8 mm) were isolated in separate compartments of a cage for the entire summer of 1957. Since most drills were insufficiently developed to be sexed when the experiment was begun, some pairs may have been of mixed sex. Also, mature males (heights 23.1 and 23.2 mm) were paired with 2 age-group I females (14.1 and 17.1 mm) in this cage. No embryo cases were deposited by any age-group I females in these tests though many were deposited by older caged drills. In addition, females less than 19 mm were never observed depositing embryo cases.

It was not determined what proportion of females is mature during the spawning season of their 3rd summer of life.

Tables I and III show the extensive range of heights of mature females. Since there is good evidence that females cease growth at sexual maturity, this suggests considerable individual variation in growth or age at maturity. The minimum height of mature *E. caudata* in the experimental area appears to be about 19 mm for females and 16 mm for males. Preliminary data obtained from examination of the gonads of large numbers of drills show that males mature at a younger age than females.

Sex ratio

Sex ratios were obtained by examining drills collected on traps. Age groups were not recognized in 1956; hence, sex ratios of different year classes could not be determined. Ignoring age differences, the July, August and September samples show a nearly 50:50 ratio, but samples in the 2 succeeding months contained significantly more females (Table IV). In 1957, considering age-group II+ only, males were slightly in predominance in May, but beginning in June in each month until September a larger proportion of females came to the traps (Table V).

TABLE III. Sizes of females which deposited embryo cases in cages or on traps

Total height (mm)	No. of Individuals	
	1956	1957
19.5	3	1
20.5	3	3
21.5	7	4
22.5	10	0
23.5	12	7
24.5	12	5
25.5	8	6
26.5	3	6
27.5	1	2
28.5	0	3
29.5	0	0
30.5	0	0
31.5	1	0
32.5	0	1
Total	60	38

TABLE IV. Sex ratios of 1956 trap samples (Age-group O not included)

Date	Uncertain	♀♀	♂♂	Total	% ♀♀
July 8	8	38	37	75	50.6
Aug. 6	7	34	41	75	45.3
Sept. 3	4	58	46	104	55.8
Oct. 8	0	25	10	35	71.4
Nov. 14	0	24	6	30	80.0

TABLE V. Sex ratios of 1957 trap samples (Age-group II+ only)

Date	Uncertain	♀♀	♂♂	Total	% ♀♀
May 8	1	25	39	64	39.0
May 11	0	9	27	36	25.0
May 13	0	15	29	44	34.6
May 15	0	20	23	43	46.5
May 22	0	31	33	64	48.4
June 5	0	21	18	39	53.8
June 18	0	46	29	75	61.3
July 4	1	31	19	50	62.0
July 17	0	15	6	21	71.4
July 31	0	30	9	39	76.9
Aug. 20	0	5	0	5	100.0
Sept. 4	0	7	6	13	53.8
Sept. 26	0	5	4	9	55.5
Oct. 9	0	11	13	24	45.8
Oct. 25	0	4	0	4	100.0

The percentages of females occurring on the traps appeared to follow the seasonal cycles of copulation and spawning (Figures 10C and 11C). It is possible that the sexes move to shells or traps in about equal numbers, copulate, and when copulatory activity wanes and spawning begins, larger and larger numbers of females move to shells in traps which provide sites for their embryo cases free from siltation. Females apparently have a greater tendency than males to move to shells projecting above the bottom, particularly during the spawning season, and this results in selective sampling by traps. Samples taken after July 31 are probably too small to be significant but nearly equal numbers of each sex in the October 9 sample may be a result of the fall copulating period. Unfortunately, many age-group I drills could not be sexed in 1957 because they were too immature, thus sex ratios were not determined.

In English waters, both Cole (1942) and Hancock (1959) found sex ratios of *U. cinerea* unbalanced in favor of females during the spawning season.

Evidence against sex reversal

Nineteen females and 21 males isolated on May 16, 1956 survived to August 31, 1957, sixteen months later, and retained their sexual identities. Eight other females and 7 males, isolated for periods of 3 to 14 months, had not changed sex at the end of the period.

Examination of external reproductive organs of drills and smears of gonads of over eight-hundred males and females gave no evidence of actual or potential hermaphroditism. Mature females possess yellow, white or orange gonads with large lobes containing vitelline bodies. Mature males possess large penes, yellow or orange gonads with small lobes containing spermatozoa, and usually swollen vasa deferentia. Neither contained organs or parts of organs typical of the opposite sex.

Copulation and overwintering of spermatozoa

To copulate, the male usually assumes a position on the lower right side of the female with his siphonal canal pointing in the same direction as hers (Hargis and MacKenzie, in press). His foot, after extending to the rim of the mantle cavity of the female, forms a groove in its anterior end through which the penis is inserted through the mantle cavity and into the vagina. Actual copulation lasted as long as 4 hours and 39 minutes. Most pairs copulated, ceased for a few hours, and then resumed intermittently for 24 to 48 hours. Promiscuity appears to be a natural phenomenon because drills in aquaria and cages copulated repeatedly with various partners. Hancock (1959) indicates that *U. cinerea* is polygamous. Often a trio of *E. caudata,* 2 males copulating with one female at the same time, was seen. Figure 10 B and C shows that copulation begins early in April and ends early in July, but occurs again through October. In cages copulation was much less intense in 1957 than in 1956.

Females collected from the experimental area and cages in late fall deposited cases with viable embryos the next spring, and thus these drills appear to retain spermatozoa for at least 6 months.

Seasonal activity

Little is known of the seasonal activity of individual gastropods. To study this aspect of their

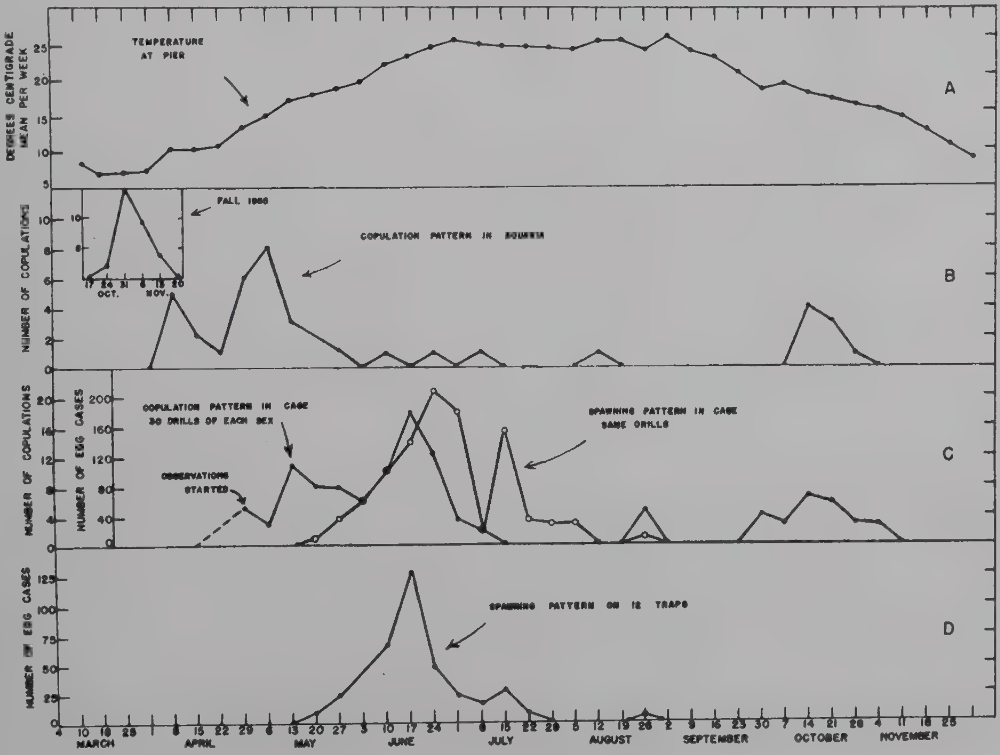

FIG. 10. Seasonal patterns, grouped by weeks, of temperature, copulation, and spawning in 1956.

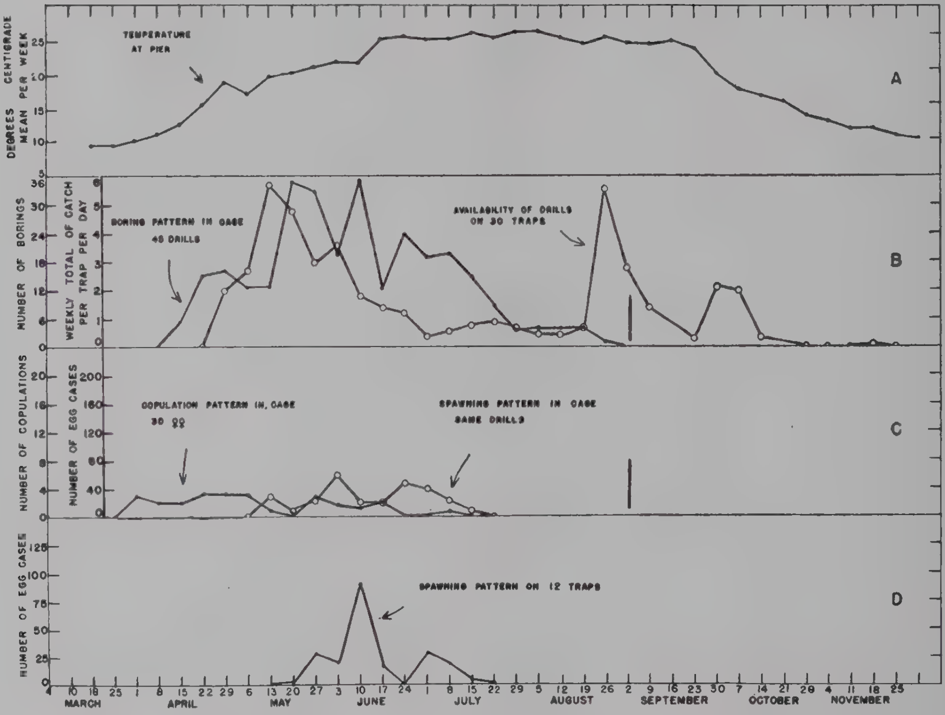

FIG. 11. Seasonal patterns, grouped by weeks, of temperature, boring, trap catches, copulation, and spawning in 1957. Solid vertical bars indicate termination of observations.

behavior, 45 *E. caudata* individually marked with a fast drying paint on March 2, 1957 were placed in a cage which was lifted at 2-day intervals to record copulation, deposition of embryo cases and drilling. A pair in copulatory position was recorded as copulating if the male's penis or copulatory groove could be observed; drilling was recorded if the snail was located over a freshly bored hole; positive identification of spawning was often uncertain, but a female seen amidst a cluster of new cases in the normal case laying position was considered the one which deposited them. The cage was examined 75 times from April 4 to September 6.

Figure 11C shows that copulation, which began 2 weeks before boring, was the earliest recorded activity. Later, copulatory activity of both sexes was interspersed with feeding. Only 3 females were observed depositing embryo cases during this period. Reduced spawning in cages corresponded to reduced spawning in natural populations during the same period. One female may have copulated after depositing embryo cases. Over half the females were not observed copulating during the period and several drills were not seen boring. On the average, females were found drilling 7 times during the 75 observations, but males only about 3 times. Drilling and feeding normally persists for several hours or days, and it is likely that most of this activity was seen and probable that these differences are normal. Actual copulation, which lasts at most only a few hours, was undoubtedly missed in most individuals.

In 1957, traps with new seed oysters from the James River were placed in the experimental area in late March and records of their catches were kept the entire summer. Catches were negligible until the week of April 29 when the mean weekly water temperature rose from 15.8°C to 19.2°C (Fig. 11B), then increased steadily to the week of May 13 (20°C), thereafter declined steadily to July 1, and only small numbers of drills came to traps until August 26. Most traps were then rebaited, and large catches were recorded again. Several traps were left with the original oysters, and the catches remained very low although they did increase slightly. Data collected by Dr. J. L. McHugh show that catches of *U. cinerea* on traps, baited with oysters not changed during summer, were smaller in July and August than in spring and fall. This pattern seems to support the work of Janowitz (1957) who found that drills are more attracted to growing oysters. McHugh (personal communication) states that maximum oyster growth at Gloucester Point occurs in spring and fall. Soon after rebaiting traps, catches diminished quickly as the smallest seed, barnacles, and mussels were consumed. The catch of September 23 was about equal to the low catches of July 1 through August 19. Traps were rebaited again on September 26, but succeeding catches were less than half those of August 26, undoubtedly because of decreased activity caused by lower water temperatures. Again the catch dropped off quickly and drills were scarce after the week of October 7 as water temperatures dropped below 17.8°C. Clearly these observations support those of Stauber (1943) and McHugh (1957) who also report that rebaited traps catch more drills. These catch records and cage observations show that this species is active only for about 6 or 6½ months a year. Andrews (1956) found that *E. caudata* came on traps only for about 6 months at Wormley's Rock in the York River.

Drilling observations in the cage were compared with weekly trap catches (Fig. 11B). Caged animals commenced boring at a temperature of 12.5°C, about 2 weeks before drills came on traps; thereafter, boring activity in cages lagged a week or more behind similar activity in nature. Boring and catch intensities paralleled each other roughly, however, and both diminished to a low point during the first part of August. Since large catches were obtained the week of August 26, after traps had been rebaited, drills presumably were still partially active; probably decreasing catches and reduced frequency of boring in July and early August largely mirror decreasing attractiveness of bait rather than inactivity or aestivation. No experiments were conducted, however, to determine whether general activity decreases during mid-summer.

Spawning period

Spawning periods of drills were studied by Engle (1935) in Delaware Bay and Andrews (1956) in the York River. Both recorded the numbers of *E. caudata* and *U. cinerea* embryo cases in drill traps. In Delaware Bay cases were deposited during the period May 23 to July 25, with greatest numbers during the week of June 13. Perhaps because his sample was smaller (110 cases), Andrews (1956) found the duration of spawning even shorter, June 13 to July 18. These workers found that the spawning period of *U. cinerea* begins earlier in spring and extends later into summer than that of *E. caudata*. Other studies on *U. cinerea* have reported a 2nd smaller spawning in some summers with a peak usually in September (Galtsoff *et al.* 1937, Cole 1942, Stauber 1943).

Embryo cases at Gloucester Point were collected in traps and a cage. During 1956, 12 traps were examined between the laboratory and ferry piers. Spawning began on traps and in the cage about May 20 at a temperature of 18.3°C (Fig. 10C and D), reached a peak during the week of June 17 when the mean temperature was 25.5°C, and ceased late in July. In the cage the peak occurred about one week later and spawning ceased in early August. A small flurry of spawning on August 26 as shown in figure 10C may have been stimulated by the slight decrease in temperature.

In 1957, 15 traps were set out in each half of the experimental area. Spawning began in the cage on May 13 at 20.0°C and on traps about May 20 at 20.6°C (Fig. 11C and D). There was no distinct peak in the cage and spawning was much less intense than in 1956. Seventy-eight cases were deposited when the traps were placed in a new section of the experimental area for 3½ days during the week of June 12. This one record for a half-weekly period is twice as high as that of any other full week and therefore may be abnormal. Hargis (personal communication) reports that numbers of embryo cases of *E. caudata* in comparable eelgrass areas were negligible in 1957 as compared to 1956. The effects of decreased spawning in 1957 became apparent when no identifiable drills of age-group O were collected on traps until October 3. In marked contrast, many small drills had already been collected by late August and September in 1956.

These spawning periods agree with those observed by Engle in Delaware Bay but are more extensive than those recorded by Andrews. There was no late wave of spawning of *E. caudata* embryo cases as reported for *U. cinerea*.

Embryo case deposition may be interrupted or inhibited by the frequent examination of traps or by unsuitable oysters within traps resulting in low numbers of cases. As an example, only 5 clusters (49 cases) were obtained from 15 traps in the down river half of the experimental area in 1957; whereas on shells, a few hundred cases were collected from that area. New cases were also collected on shells after spawning ceased on traps.

Intensity and duration of embryo case production

Previous studies of intensity and duration of embryo case production in *U. cinerea* are of limited value because the actual numbers of females under observation were not known (Carriker 1955). Various authors have estimated that *U. cinerea* females deposit about 25 to 50 cases a spawning season. Nelson (1922), Engle (1940), Cole (1942), and Hancock (1959) state that *U. cinerea* do not deposit all their cases at one time, but may lay several clusters in a spawning season.

Because nothing was known of this phase of reproductive activity for *E. caudata,* experiments were designed to determine the numbers of cases deposited by individual females of various heights. Pairs of females and males graded from the smallest to the largest available were put into compartments of 3 cages on May 16 before spawning had begun. The compartments of a 4th cage housed pairs each about 20 mm in height. Several one- and 2-year-old oysters were placed in each compartment. Cages were cleaned weekly when embryo cases were counted. The experiment was continued in 1957 with the same animals, but with new oysters which were not changed during the summer unless they were completely consumed. Missing or dead animals were replaced by May 11, 1957. The cages were examined and cleaned periodically during the winter.

TABLE VI. Duration and intensity of spawning by individual caged females

Year	Initial Height (mm)	Duration (weeks)	Number of weeks inactive	Total embryo cases
1956	19.4	8	2	63
	20.7	8	1	61
	21.1	7	0	95
	22.0	1 cluster**	0	2
	23.3	8	1	46
	24.0	4	1	17
	24.1	10	3	45
	25.7	5	0	37 or 38
	26.7	6	1	25 or 26
	27.8	2	0	29
	29.0	8	1	95
		6		
1957	19.7	7	2	54
	20.0	3	1	15
	21.7	11	0	174
	23.0	4	1	37*
	23.0	5	0	49
	23.7	4	0	64
	23.7	1 cluster**	0	9
	23.8	6	2	71
	24.3	10	4	71
	24.4	8	3	45
	24.7	6	0	68
	24.8	8	2	79
	25.2	2	0	14
	25.3	3	0	22
	25.4	9	1	114
	25.7	7	2	28
	26.0	1 cluster**	0	3
	26.0	8	1	76
	26.3	7	3	60
	27.6	12	4	107
	32.3	4	0	57
		6		55 (1956 & 1957)

* Lost June 8 and excluded from mean.
** Called duration one week.

Number of embryo cases

The mean number of embryo cases per season per female was 55 (range 2 to 174, Table VI). Apparent differences in embryo case production in the 2 years may not actually mirror conditions in the experimental area for differences may have been caused by factors such as kinds and amounts of food which were not carefully controlled (Table VII). Also, it is not known if fertility of males changes with time.

TABLE VII. Comparison of the total number of cases deposited by the same females in successive years

Serial number of drill	1956	1957
1	61	54
2	63	45
3	95	15
4	29	60
5	25 or 26	22
6	46	9
7	45	71
Mean	52	39

Females retained from 1956 and reproductively active for the first time in 1957 laid an average of 77 cases. Two females that deposited cases in 1956 did not do so in 1957.

The number of cases females in the experimental area deposit was not determined. However, sizes of clusters found on the bottom were about the same as those deposited by caged females (Table VIII). One hundred and thirty-six clusters containing about 10 cases each were deposited by 23 caged females in 1957. The mean number of embryo cases contained in 232 clusters from shells collected randomly in the experimental area was about 9. Observations of particular compartments over a period of a few weeks showed that females deposited small clusters of cases, desisted for a short period and later resumed this activity.

TABLE VIII. Comparison of numbers of cases per cluster on shells in the experimental area with those deposited by caged females, summer 1957

No. of cases per cluster	Cages hauled each week	Natural bottom	Cage hauled every two days*
1-5	31	31	49
6-10	44	80	26
11-15	49	51	8
16-20	8	18	2
21-38	5	6	0
Totals	136	232	85

* Not compared in text with other two distributions.

Females deposited an average of 6 clusters (range one to 18).

The number of cases deposited by a female is apparently independent of her size. Of 31 females that deposited cases in captivity the smallest 14 laid an average of 58.2 cases, the largest 17 an average of 51.5. The difference is not statistically significant. ($\chi^2 = 0.03$, d.f. $= 1$, $P = 0.86$).

Spawning duration of individual females

Duration of the spawning period for individual females cannot be stated with precision because cages were examined only once a week. In 1956 the average duration for 11 females was approximately 6 weeks. In 1957 for 20 of 21 identifiable females it was also 6 weeks (Table VI). The spawning period in the experimental area lasted approximately 9 weeks in 1956 and 8 weeks in 1957 (Figs. 10C and 11C). These cage data thus indicate that a single female may spawn throughout most of the spawning season.

Substratum of embryo case deposition

Types of substratum females select for depositing embryo cases were determined from 3 large hand-picked collections of shells and other objects with attached cases from the experimental area and from cages and aquaria. The most common shells in this area were dead hard clams or live clams partly exposed, and dead and live oysters. These shells supported jingles *Anomia simplex,* worm tubes *Hydroides* sp., and often growths of red sponge *Microciona* sp. Cases were always attached to hard surfaces and no preference for jingles, worm tubes, or the clam or oyster shell itself was obvious. Cases were also found on dead jingles, short razor clams *Tagelus plebius,* stones and bottles. Uncommonly, cases were found on live *E. caudata, U. cinerea, Anadara ovalis,* and *Modiolus demissus,* dead *Anadara transversa,* live and dead *Balanus* sp., and bases of eelgrass blades. In the laboratory they were found on wood, plastic screen and sheeting and metal tacks. The only evident requirements for these substrata are that

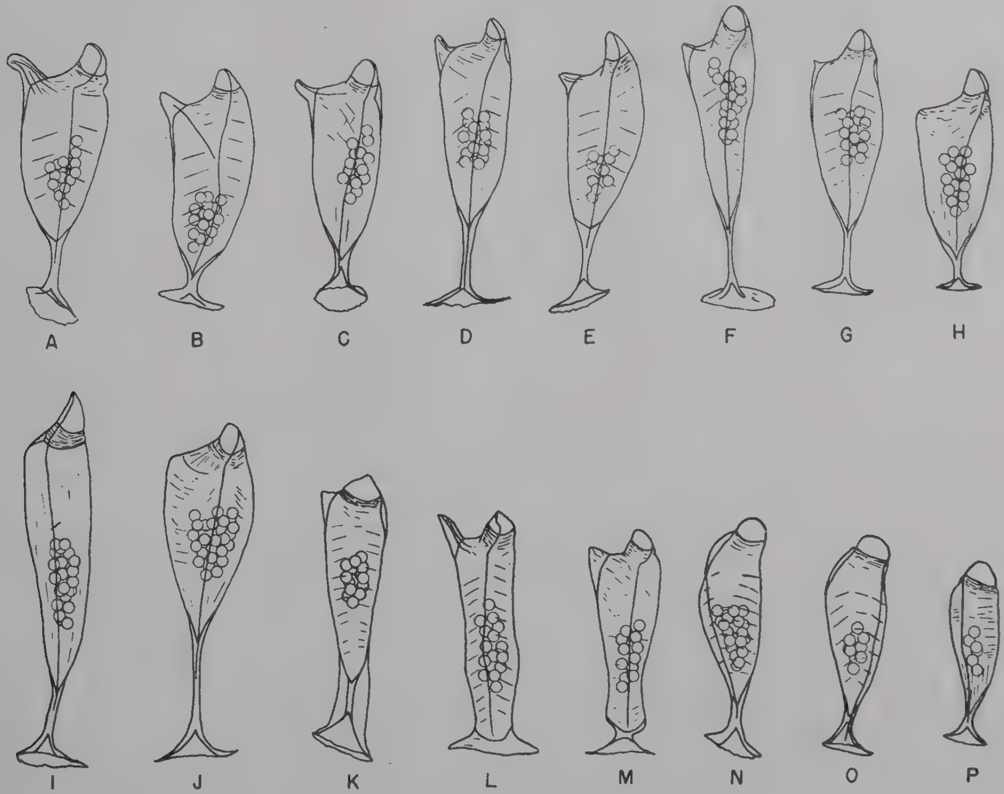

FIG. 12. Variation in shapes of *E. caudata* embryo cages collected in the vicinity of Gloucester point. X5.3.

A to H —Usually shaped cases
D —Most common shape
I to P —Unusual shapes
K —Stalk with odd wing-like protuberances
N to P —Cases with no secondary projection

they be hard and free of fouling. Occasionally *U. cinerea* cases occurred in similar sites. Most cases were deposited upright in a vertical or slightly tilted position, but a few were found distal end down. Because *E. caudata* does not climb appreciably, no cases were found on eelgrass blades or pier pilings, where *U. cinerea* cases occur in numbers.

Since new clusters were deposited in various places about cage compartments which held one female, it is apparent that females do not necessarily return to their old spawning sites to deposit cases.

Description of cases and embryos

Embryo cases of *E. caudata* are leathery, vase-shaped capsules with 2 distal projections which make them easy to distinguish from cases of other local gastropods. The larger projection is a hemispherical operculum which covers the aperture through which hatching conchs will emerge, the smaller is a solid extension of case material. The case itself is triangular in cross section. A longitudinal seam or suture extends from one side of the stalk distally along one triangular edge of the case over the operculum, dividing it into halves, and down the middle of the broad side to the opposite side of the stalk. Similar sutures in embryo cases of muricids *Thais lapillus* and *Ocenebra erinacea* were described by Fretter (1941), and in *U. cinerea* by Hancock (1956). Figure 12 illustrates variability in shapes of cases. The secondary projection is not always present and the seam does not always occur in the same plane of each case, although it always runs over the middle of the operculum. A few anomalous cases were observed with sections of walls missing, but with embryos still in normal position.

The color of cases changes with time. When first deposited they are almost translucent except for the opaque cap. They do not have the bluish cast described by Pope (1910-11), Carriker (1955), and Ganaros (1957) for cases of *U. cinerea.* In 2 or 3 weeks the color changes to deep yellow, and after the conchs have emerged, to dark brown. Cases from the experimental area averaged, in mm, 7.7 in height (6.0 minus stalk), and 1.8 in width. Range in height was 5.2 to 11.0. Cases collected at Tillage's oyster ground averaged 9.2 (6.9 minus stalk), and 2.4 wide, and ranged from 7.4 to 11.3 in height.

Whenever a female was observed depositing cases, measurements were made of her height and height of the cases. As Hancock (1959) found with *U. cinerea,* usually larger females deposit larger cases but in *E. caudata* there is considerable variation (Table IX). Perhaps measurement of the soft parts of the drill such as dimensions of the foot would have shown a closer correlation between her size and size of embryo cases she deposits.

TABLE IX. Relationship between shell height of *E. caudata* females and mean height of embryo cases they deposited, summers of 1956 and 1957 (Caged and natural populations)

Height of female (mm)	Height of cases (mm)	Numbers of cases
20.1	6.5	59
20.5	6.4	41
21.1	7.1	48
21.1	7.8	6
22.2	7.5	14
23.4	8.0	25
23.5	7.7	2
24.0	7.1	6
24.1	8.2	3
24.3	9.0	14
24.8	7.2	26
25.4	8.2	25
26.0	9.9	10
26.5	9.1	8
26.8	7.9	18
26.9	8.1	14
27.5	8.2	19
28.0	7.5	6

Measurements were made of most cases deposited by known caged females in 1956. Mean height for the first half of individual spawning seasons was 7.3 mm. Mean height in the 2nd half was 7.0 mm. The difference was not significant statistically ($\chi^2 = 32.45$, d.f. $= 22$, $P = 0.08$); therefore, there is no evidence that size of embryo cases changes during the spawning season.

Within freshly-laid cases, embryos form a loose clump suspended in a clear jelly-like substance. Early embryos are spherical and most are pale yellow, though many are white. A few are yellow, light tan, light orange or purple. Carriker (1955) stated that *U. cinerea* embryos are yellow to orange in color. Necrotic embryos usually turn purple. Live, apparently normal, protoconchs with purple vitelline bodies were seen occasionally. When locomotory organs develop, embryos move about within the case until they hatch, but late protoconchs often become so crowded that movement is impeded.

Forty-two freshly-laid embryos averaged 0.36 mm (range 0.34-0.39) in diameter, the same size reported by Carriker (1955) for *U. cinerea* embryos. Fifty-four hatching conchs, measured as they emerged from the apertures of cases, averaged 0.9 mm (range 0.7-1.1) in greatest height. The conchs are not pelagic and after emergence they crawl down the sides of their cases and about the substrate to which the case is attached. Tubular noncoiled individuals, looking otherwise nor-

TABLE X. Numbers of embryos per case in various samples collected at Gloucester Point and Tillage's oyster ground (summer 1956 and 1957)

Location	Source	Date	No. of cases	Embryos Per Case		
				Mean	Range	Variance
Experimental area	handpicked shells	May 28-30, 1957	277	12.6	1-24	17.0
" "	" "	Jun 15-17, 1957	349	13.5	2-27	16.2
" "	" "	Jul 1-22, 1957	166	13.3	1-27	18.4
" "	buoyed traps	May 28-Jun 28, 1956	210	15.8	5-35	27.7
" "	" "	Jun 1-Jul 19, 1957	187	14.5	6-32	27.4
Cage, experimental area	cage	May 24-Jun 30, 1956	262	15.2	2-32	23.6
Cage, large mixed local and Wormley Rock drills	"	Jun 9-Jul 4, 1956	184	21.2	10-37	23.3
Tillage's oyster ground	dredged oysters	May 13-Jul 2, 1956	157	18.4	6-36	30.9
" " "	" "	Jun 13, 1957	283	20.2	3-34	20.1
" " "	cage	Jul 3-24, 1956	90	19.5	8-47	49.4

mal, appeared occasionally. Although somewhat similar, late stage protoconchs of *E. caudata* from this area differ from those of *U. cinerea* in that the siphonal canal is less heavily-tinged with purple; the 2 protoconchs can usually be distinguished by this character.

Number of embryos per case

In 1935 Haskin showed that *E. caudata* in Cedar Creek, Barnegat Bay, New Jersey, deposited more embryos per case than *U. cinerea*. In traps and cages, 445 cases average 22.2 embryos each (range 8 to 42), and 1,297 *U. cinerea* cases averaged 8.1 embryos each (range 0 to 20). According to Carriker (1955), 6 similar studies of *U. cinerea* report averages varying from 8.0 to 11.0 embryos per case.

In this study, 10 samples of cases (Table X) were collected during 1956 and 1957 to determine whether (1) the numbers of embryos per case change during one spawning season, (2) there are annual variations in a particular area, (3) there are local differences between drill populations in a particular area, and (4) there are differences between caged and wild drills. The results were not conclusive except to show a clear difference between the experimental area and Tillage's ground, which suggests that there are local differences in numbers of embryos per case. Hancock (1959), working on *U. cinerea* in English waters, found quite marked differences in numbers of embryos per case from one location to another.

A small number of selected large females held in a cage deposited an average of 21.2 embryos per case, about 7 above normal for the experimental area, which suggests that characteristics of the female, rather than environmental factors, may be the more important factor controlling numbers of embryos per case.

Similar to the findings of Hancock (1959) who found that there is considerable variation in numbers of *U. cinerea* embryos per case deposited by a single female, records of individually caged *E. caudata* females also demonstrate considerable variation in this attribute (Tables XI and XII).

TABLE XI. Variation in numbers of embryos per case deposited by individual caged females, summer 1956

Female	Number of cases	Mean	Variance
A	58	11.9	5.5
B	43	9.9	6.8
C	79	8.2	3.1
D	29	20.8	11.7
E	59	10.0	4.8
F	19	18.1	16.3
G	23	14.4	6.8
H	28	16.5	20.4
I	26	10.3	3.7

TABLE XII. Variation in numbers of embryos per case deposited by female B in table 11

Number of embryos	Frequency
4	1
5	2
6	1
7	3
8	4
9	11
10	4
11	6
12	3
13	6
14	0
15	1
16	1

Incubation period

Knowledge of the incubation period of *E. caudata* embryos may be useful in developing control measures involving destruction of embryo cases. Several workers have collected data on this subject for *U. cinerea* in other areas, and their results vary widely. The most careful work has been done by Haskin (1935), Cole (1942), and Ganaros (1958).

Haskin (1935), working in Barnegat Bay, held embryo cases in field cages at temperatures ranging from 23.3°C to 29.1°C, and reported incubation periods lasting from 18 to 25 days. Cole (1942), in England, found incubation periods of 27 to 32 days when cases were held in the laboratory at temperatures averaging 22.6°C. At Miliford, Connecticut, Ganaros (1958) determined incubation periods of embryos held in the laboratory at constant temperatures. The first conchs held at 20°C were released in 30 to 43 days; those held at 25°C, in 22 to 38 days.

Embryo cases of *E. caudata* were collected from traps and a cage every 2 days, left on their original substratum, and placed in clear perforated plastic cups suspended from the laboratory pier in a tray one foot from the bottom. Two or 3 clusters containing several cases each were used for most determinations. Cases were examined every 2 days for hatching embryos. Termination of the incubation period was defined as the time when over one-half the cases in a particular cluster had released at least one conch. Although a slightly uneven rate of development was observed, no attempt was made to record incubation periods of individual embryos.

To determine whether holding cases in perforated plastic cups influenced incubation periods, oysters bearing cases were attached to a rectangular wooden board by elastic bands. Because the board collected algae, tunicates, and silt, it closely resembled the bottom.

Table XIII shows that there was close agreement in hatching times of embryos in different clusters of the same age, and that holding cases in perforated cups apparently did not influence the

TABLE XIII. Incubation periods of *E. caudata* embryos

	Site	Date laid	Number of cases	Hatching date	Incubation period (days)	Temperature During Period (°C)	
						mean	range
1956	Cup	May 18-23	—	June 15-17	24-31	21.1	18.3-24.7
	"	May 28-30	—	June 19-21	21-25	23.4	19.2-24.7
		May 28-30	—	June 19-21	21-25		
		May 28-30	—	June 19-21	21-25		
	"	June 11-13	12	June 29-July 1	17-21	24.7	21.9-26.9
		June 11-13	10	June 29-July 1	17-21		
		June 11-13	21	June 29-July 1	17-21		
	"	June 18-21	13	July 5-7	15-20	25.4	21.9-27.5
		June 18-21	8	July 5-7	15-20		
		June 18-21	3	July 5-7	15-20		
	"	June 27-29	4	July 13-15	15-19	26.0	25.0-27.5
		June 27-29	7	July 13-15	15-19		
	"	July 5-7	4	July 20-24	14-20	25.6	25.3-25.8
		July 5-7	6	July 20-24	14-20		
	"	July 14-16	11	July 29-31	14-18	25.7	25.0-26.1
		July 14-16	5	July 29-Aug. 1	14-19		
		July 14-16	—	July 29-Aug. 1	14-19		
	"	July 24-26	5 or 6	Aug. 10-12	16-20	25.4	24.4-26.4
		July 24-26	5 or 6	Aug. 10-12	16-20		
1957	Cup	May 14-16	14	June 6-8	21-25	21.7	19.4-23.1
	Board	May 14-16	10	June 6-8	21-25		
	Cup	June 15-17	5	June 28-July 1	12-17	26.2	24.7-27.2
	Board	June 15-17	6	June 28-July 1	12-17		
	Cup	June 24-26	9	July 8-10	13-17	26.1	25.3-26.7
	Board	June 24-26	6	July 8-10	13-17		
	Board	June 24-26	16	July 8-10	13-17		
	Cup	July 4-6	13	July 19-21	13-17	26.4	25.8-26.9
	Board	July 4-6	12	July 19-21	13-17		
	Board	July 14-16	6	July 30	14-16	26.6	25.8-27.5

incubation period. Incubation periods lasted 24 to 31 days at a mean temperature of 21.1°C and shortened as the temperature increased, *e.g.* at 26.5°C it lasted only 15 to 17 days. Probably as a result of higher temperatures in 1957, incubation periods were shorter than in 1956. Incubation periods for *E. caudata* were 5 to 6 days shorter than those reported for *U. cinerea.*

Percentage of embryos reaching protoconch stage

Unlike *Thais lapillus* and other related gastropods (Korschelt and Heider 1890), *E. caudata* females do not include nurse embryos (nourishing eggs) within their cases. Portman (1926) and others believe that nurse embryos are produced by fertilization of normal ova by atypical spermatozoa. Evidently such embryos fail to develop normally and serve as food for normal embryos. Nurse embryos were not seen in the almost 3000 cases studied, and microscopic examination of gonad smears of hundreds of males of *E. caudata* showed only one type of spermatozoon.

To establish the numbers of embryos that successfully attain the prehatching or protoconch stage, embryos in 37 freshly-deposited cases were counted by carefully manipulating cases under the lens of a binocular microscope. Cases were then isolated in separate compartments of a plastic box held in an oyster tray suspended in the York River. An average of 93% (range 82-100) of embryos in these different cases developed fully and the numbers of embryos at various embryonic stages were similar in 361 embryo cases deposited in cages.

Predators and associates of embryo cases

Large numbers of cases from the experimental area were devoid of embryos even though the operculum was still in place. Closer observations revealed holes in the sides of these cases, the most common of which was a C-shaped slit about 0.8 millimeters in diameter and, therefore, large enough to serve as possible exit for emerging conchs. At least one case with a slit still contained undeveloped embryos which indicates that predators made the slits. No evidence beyond this, however, was obtained to show whether C-shaped slits are made by the conchs themselves or by predators. Less frequently, round or oval holes of varied sizes, always too small to permit the exit of conchs, were seen. Occasional cases bore jagged tears and in some of these most of the case was torn away. In the laboratory, mud crabs (Xanthidae) made similar jagged tears. Some clusters exhibited all three kinds of damage and often more than one slit or hole was seen in a single case. Since 19 to 42% of cases in samples were damaged, predation, if this accounts for all damage, may be an important factor in limiting the size of drill populations in the experimental area (Table XIV). It is possible that predators of cases may be non-selective and prey on embryos at all stages of development. If so, many embryos still not hatched in the cases collected might have been destroyed in like manner had they been left on the bottom.

Hancock (1956) in England showed that if embryos of *U. cinerea* as old as unshelled veligers are removed from their cases, the operculum of these cases will eventually come free. The operculum will not come free if younger embryos are removed. If this is also true for *E. caudata*, it probably explains the finding of some damaged cases with their opercula missing. It seemed possible that predators might have entered empty as well as full cases; instead, they probably fed on unshelled veligers or protoconchs.

A substantial but incomplete list was made of plants and animals observed on *E. caudata* embryo cases during the summers of 1956 and 1957 (Table XV). The scale worm *Lepidonotus sublevis,* an active predaceous annelid, is one of the possible predators, though it did not appear to be common. Its scarcity, however, may be due to its ability to escape collection with cases or it may not be abundant in this area. Perhaps only a few are required to do significant damage. An as yet unidentified polychaete worm which builds a tube on embryo

Table XIV. Numbers of damaged and undamaged embryo cases collected by handpicking shells in the experimental area, summer 1957

Sample	Number Damaged					Number Undamaged						
	C-shaped slit	Hole	Tear	Not determined	Total	Pre-veliger stage	Unshelled veliger stage	Pro-toconch stage	Embryos hatched	Total	Total Cases	% damaged
June 15	52	21	17	15	105	135	107	113	85	440	545	19.3
June 17	179	44	0	8	231	49	127	115	43	334	565	40.1
June 26	37	6	14	0	57	52	0	16	12	80	137	41.6
July 1-22	12	9	28	0	49	15	13	2	69	99	148	33.1

cases also is suspected. *Caprella* was seen commonly about cases but did not damage them in the laboratory. Possibly the gastropods *Bittium alternatum,* small *U. cinerea, Mitrella lunata, Odostomia impressa,* or other gastropods, worms or small arthropods common on oysters and eelgrass, but rarely seen on cases, perforate them. Occurring commonly on cases with slits or holes, often several on one drill case, were embryo cases of 2 small gastropod species. In the laboratory these cases released pelagic veligers which did not survive to a stage that could be identified.

Table XV. Plants and animals observed attached or clinging to *E. caudata* embryo cases

	Occurrence
Ulva sp.	Common
Small filamentous multicellular brown algae	Common
Various diatoms	Abundant
Folliculina moebiusi	Rare
Zoothamnium sp.	Abundant
Yellow sponge	Common
Red sponge on base	Rare
Sea anemones	Rare
Nematodes	Abundant
Feather-duster worms (two species)	Rare
Lepidonotus sublevis	Rare
Unidentified burrowing polychaeta	Common
Young *Balanus* sp.	Once
Caprella sp.	Common
Bittium alternatum	Rare
Urosalpinx cinerea early conch	Rare
Mitrella lunata near base of cases	Rare
Odostomia impressa	Rare
Three types of gastropod embryo masses	Two very common; one rare
Colonial bryozoa	Common
Molgula sp.	Rare

Folliculina moebiusi, the bottle animal, occurred on several cases in one cluster. *Zoothamnium,* a colonial protozoan, occurred in large numbers on many. A yellow sponge was seen commonly around the bases but few clusters were completely covered by it. Small anemones were seen 3 or 4 times. Nematodes and diatoms were abundant in the detritus which collects on cases. Two species of feather-duster worms which make coiled tubes occurred only rarely. A young barnacle was also observed. Cases were commonly partially encrusted with colonial bryozoa, and young *Molgula* were occasionally attached. Probably none of the above listed organisms except the yellow sponge seriously impedes development of *E. caudata* embryos.

Summary and Conclusions

Eupleura caudata, a boring snail that occurs in considerable numbers in some parts of Virginia and elsewhere along the Atlantic coast, has been investigated only spasmodically, usually in conjunction with investigations of the more widespread *Urosalpinx cinerea.* Recent studies at the Virginia Fisheries Laboratory have made it possible to outline the life history in some detail.

Because in winter few drills can be collected on traps and caged animals are dormant, it is believed that *E. caudata* hibernates. Drills in the York River become active and begin copulating in April as temperatures rise to over 10°C. Individual copulatory acts may last about 4 hours but couples often remain paired and copulate intermittently for 24 to 48 hours. There is good evidence to show that sexual promiscuity occurs. Sex ratios obtained from trap catches indicate that equal numbers of males and females move to shells projecting above the bottom during this period. Spawning begins in late May when temperatures reach 18 to 20°C, reaches a peak in June and early July (21.1° to 26.1°C), and ceases for the year about the beginning of August. During the spawning period, females come to traps in greater numbers than males. Copulation ends early in July, but is resumed in fall as water temperatures decline to about 21°C, and ceases for the year at about 16.7°C. Since females isolated after this period are capable of depositing cases with living embryos, it seems probable that this fall copulatory period serves to insure that females, particularly in sparse populations, have spermatozoa for spawning the following year.

Mature females in cages deposit an average of 55 embryo cases over an average period of 6 weeks, almost the full extent of the spawning period. Cases in the experimental area are deposited primarily on dead and live hard clams, oysters, and jingles. Most clusters include 8 to 10 cases, containing an average of 14 embryos. Ninety-three % or more of these embryos reach the protoconch stage and probably all protoconchs hatch. In the absence of predation, therefore, a mature female may produce 700 young conchs each summer. At the time of peak spawning in mid-June, the incubation period is from 12 to 20 days. Thus, the greatest emergence of conchs occurs during the first week of July when oysters begin setting at Gloucester Point (Andrews 1955).

Growth of newly hatched drills, which emerge at a height of about 0.9 mm, is apparently rapid, for their mean height on October 27, 1956 was 12 mm. Females probably are not mature in their 2nd summer, but continue to grow until the 3rd when probably most attain sexual maturity and growth ceases. The onset of maturity may be governed by rate of growth rather than by age. Males also show determinate growth, but cease growth at a smaller size. With increase in age, sculpturing of shells is worn, and drills in their 2nd summer apparently can be distinguished from those in their 3rd or later years of life. By fall the new or zero year class also can be distinguished from the other 2 groups on the basis of shell characters.

Trap catches of drills rise to a peak about 3 weeks before the peak of spawning. Federighi (1931), Galtsoff *et al.* (1937), Stauber (1943) and Andrews (1956) noted a similar pattern in their studies of *U. cinerea.* As spring temperatures rise, the first activity of *E. caudata* is copulation, soon interspersed with feeding, which later becomes the dominant activity. This heavy feeding possibly provides energy and food reserves for spawning.

This study has revealed that females of *E. caudata* do not attain sexual maturity until after the 2nd summer of life. The species apparently compensates for this during and after its 3rd summer by depositing large numbers of cases containing many embryos most of which hatch. The species thus could be partially controlled by intensive eradication practices during the first 2 years of life. If predators of cases can be identified, and their numbers increased on natural bottom, or related forms with similar feeding habits introduced, control may be possible.

Another factor which may hold populations of *E. caudata* in check is the inability of drills to use eelgrass, pier pilings and other elevated structures as sources of food and embryo case attachment. Perhaps this explains the scarcity of *E. caudata* in the experimental area, an eelgrass bed with few shells, in contrast to an abundance of them on an abandoned oyster bar, Wormley's Rock, observed by Andrews (1956).

There is good evidence that the intensity of spawning varies greatly. Possibly, intensity of spawning is directly dependent upon intensity of copulation since both were high in 1956 and low in 1957 or, perhaps, spawning is affected by other factors which affect copulation in a similar way. Perhaps spawning intensity could be predicted in advance from a record of copulatory activity in spring.

REFERENCES

Andrews, Jay D. 1955. Setting of oysters in Virginia. Proc. Natl. Shellfish. Assoc. **45**: 38-46.

———. 1956. Trapping oyster drills in Virginia. I. The effect of migration and other factors on the catch. Proc. Natl. Shellfish. Assoc. **46**: 140-154.

Carriker, Melbourne Romaine. 1955. Critical review of biology and control of oyster drills. U. S. Fish. and Wildlife Serv., Spec. Sci. Rept. Fisheries, 148.

Clarke, A. H., Jr. 1956. Natural biological control of a *Mya* predator. Nautilus. **70**: 37-38.

Cole, H. A. 1942. The American whelk tingle, *Urosalpinx cinerea* (Say), on British oyster beds. Jour. Marine Biol. Assoc. **25**: 477-508.

Engle, James B. 1935. Preliminary report of the U. S. Bureau of Fisheries oyster drill control project in New Jersey. Unpublished report, U. S. Bur. Fish. Washington.

———. 1940. The oyster drills of Long Island Sound. Conv. Addr. Natl. Shellfish Assoc., New Haven, Connecticut.

Fretter, Vera. 1941. The genital ducts of some British stenoglossan prosobranchs. Jour. Marine Biol. Assoc. **25**: 173-211.

Galtsoff, Paul S., Herbert F. Prytherch, and James B. Engle. 1937. Natural history and methods of controlling the common oyster drills (*Urosalpinx cinerea* Say and *Eupleura caudata* Say). U. S. Bur. Fish. Fishery Cir. 25.

Ganaros, Anthony E. 1958. On development of early stages of *Urosalpinx cinerea* Say at constant temperatures and their tolerance to low temperatures. Biol. Bull. **114**: 188-195.

Hancock, D. A. 1956. The structure of the capsule and the hatching process in *Urosalpinx cinerea* (Say). Proc. Zool. Soc. London **127**: 565-571.

———. 1959. The biology and control of the American whelk tingle *Urosalpinx cinerea* (Say) on English oyster beds. Fish. Invest., Ser. 2, 17(6).

Hargis, William J., Jr. 1957. A rapid live-sexing technique for *Urosalpinx cinerea* and *Eupleura caudata*, with notes on previous methods. Limnol. and Oceanog. **2**: 41-42.

———**, and Clyde L. MacKenzie, Jr.** In press. Sexual behavior in oyster drills.

Haskin, Harold H. 1935. Investigations on the boring and reproductive activities of oyster drills *Urosalpinx cinerea* Say and *Eupleura* sp. Unpub. Rept. U. S. Bur. Fish. Washington.

Hewatt, W. A., and Jay D. Andrews. 1954. Oyster mortality studies in Virginia. I. Mortalities of oysters in trays at Gloucester Point, York River. Texas Jour. Sci. **6**: 121-133.

Janowitz, E. 1957. Further studies in the attraction of *Urosalpinx* by oysters. Natl. Shellfish. Assoc. Convention Paper (Unpublished).

Korschelt, E., and K. Heider. 1890. Lehrbuch der vergleichenden entwicklungsgeschichte der wirbellosen thiere. Specieller Theil. Erstes Heft. Jena, Gustav Fischer.

Magalhaes, H. 1948. An ecological study of snails of the genus *Busycon* at Beaufort, North Carolina. Ecol. Monogr. **18**: 377-409.

McHugh, J. L. 1956. Trapping oyster drills in Virginia. II. The time factor in relation to the catch per trap. Proc. Natl. Shellfish. Assoc. **46**: 155-168.

———. 1957. Trapping oyster drills in Virginia. III. The catch per trap in relation to condition of bait. Proc. Natl. Shellfish. Assoc. **47**: 83-102.

Moore, Hilary B. 1936. The biology of *Purpura lapillus*. I. Shell variation in relation to environment. Jour. Marine Biol. Assoc. **21**: 61-89.

———. 1938. The biology of *Purpura lapillus*. II. Growth. Jour. Marine Biol. Assoc. **23**: 57-66.

Nelson, Thurlow C. 1922. The oyster drill: a brief account of their life history and possible means of combating them. Appendix Rept. Biol., New Jersey State Bd. Shellfish., Nov. 1922.

Pope, T. E. B. 1910-11. The oyster drill and other predatory mollusca. Unpub. Rept. U. S. Bur. Fish. Washington.

Portman, Adolf. 1926. Le role du spermatozoide atypique dans la formation des oeufs nourriciers de *Buccinum undatum* L. Arch. Zool. Exptl. et Gen. Notes et Revue. **65:** 103-124.

Stauber, L. A. 1943. Ecological studies on the oyster drill, *Urosalpinx cinerea,* in Delaware Bay, with notes on the associated drill, *Eupleura caudata,* and with special consideration of control methods. Unpub. Ms., Oyster Res. Lab. Rutgers Univ. New Brunswick, N. J.

Weymouth, Frank W. 1923. The life history and growth of the Pismo clam. Fish Bulletin No. 7, State of California Fish and Game Commission.

———, H. C. McMillin, and H. B. Holmes. 1925. Growth and age at maturity of the Pacific razor clam, *Siliqua patula* (Dixon). Bull. U. S. Bur. Fish. **41:** 201-236.

———, and Seton H. Thompson. 1931. The age and growth of the Pacific cockle (*Cardium corbis,* Martyn). Bull. U. S. Bur. Fish. **46:** 633-641.

THE MICROBIOLOGY OF FLATHEAD AND ROGERS LAKES, MONTANA II. VERTICAL DISTRIBUTION OF THE MICROBIAL POPULATIONS AND CHEMICAL ANALYSES OF THEIR ENVIRONMENTS[1]

Louise F. Potter and Gladys E. Baker
Plant Science Department, Vassar College, Poughkeepsie, New York

Studies on the microbiology of Flathead and Rogers Lakes, Montana, which were begun in 1951 by Potter and Baker (1956), were extended during the summers of 1953 and 1954. Vertical distribution of microbial populations and chemical analyses of the water were determined for 4 locations in Flathead Lake and for 3 areas in Rogers Lake. The surveys of Graham and Young (1934) and Young (1935) included chemical analysis of Flathead Lake and information on the vertical distribution of bacteria. Brunson and Nelson (1952) and Lauff (1953) published data for Rogers Lake. This report is an extension of the available information for the two lakes which are distinctly different in the limnological sense.

It is a pleasure to acknowledge the cooperation of the Montana Biological Station, Montana State University, particularly the generous assistance of Dr. Royal Bruce Brunson in obtaining the samples. The facilities of the Botany Department, University of California, Berkeley, which were generously available to the second author during a research leave in 1954-1955, are gratefully acknowledged. The assistance of Helen H. Hughes, née Rigg, in 1953 and of Dr. Elizabeth J. Rock, who performed the chemical analyses in 1954, is acknowledged with pleasure.

Material and Methods

Three of the stations on Flathead Lake were those described previously by Potter and Baker (1956): the inlet area, Flathead Delta (FD); the outlet area, Polson Bay (PB); and a protected bay, Big Arm Bay (BA). The deep station, Yellow Bay (YB-D), was slightly west of the station used in 1951. It was 10 m deeper than the 1951 station. The 107 m depth was located by sounding in 1952 and in 1953. Because this is the deepest area known in the vicinity of Graham and Young's station 2 (Graham and Young 1934), it was selected for this investigation on vertical distribution.

Four regions for sampling were selected on Rogers Lake: Station 1, 0.5 m, between the larger *Scirpus* bed and *Carex* mat; Station 2, 1.5 m, the east side of the *Scirpus* bed; Station 3, 5.0 m, the open portion of the lake; and Station 4, the spring inlet on the west side of the lake. A map of Rogers Lake has been published by Brunson and Nelson (1952).

In 1953 the level of Rogers Lake was low compared to that of 1951. In 1954, when vertical distribution was studied, the level was intermediate between the 1953 low and the high of 1951. The inlet area, Station 4, in 1954 was shallow and no longer contiguous with the lake proper. Since little water was flowing through this station, sampling material was limited. Consequently chemical analysis was omitted.

For microbiological analyses all surface water samples were collected by scooping up water in a sterile Erlenmeyer flask. All other water samples were collected with a special sampler (Potter, Osterhoudt and Baker 1958). The samples were transferred aseptically to sterile Erlenmeyer flasks and transported to the laboratory in an insulated refrigerator bag cooled by frozen pillows of "Sno-Gel ice." Mud samples were secured with an Ekman dredge disinfected with "Roccal". The mud was placed in sterile bottles and transported

---

[1] This research was supported in part by a grant from the National Science Foundation (G-613).

to the laboratory in the refrigerator bag. In the laboratory all samples were diluted and plated with sodium caseinate agar (Fred and Waksman 1928) as soon as possible. Plates were incubated at room temperature for 3 weeks. Counts were made of the total number of microbial colonies, and the percentage of chromogens determined. Smears of 50 to 100 bacterial colonies were stained by the Hucker modification of the Gram method as described in the *Manual of Microbiological Methods* (1957). The smears were used to determine bacterial morphology. All smears were taken from plates which had been used for counting. Beginning with a colony selected at random, all colonies in a section or on a plate were sampled. Some fungi were identified as the plates were counted. Most identifications were made after transfer to other media.

The water samples for chemical analysis were obtained with a Kemmerer water sampler according to methods described by Welch (1952). Carbon dioxide and carbonates were determined by titration (Welch 1951). All other chemical determinations were completed colorimetrically with a standard Hellige water comparator. All methods for preparation and completion of analyses were those recommended for the Hellige water comparator in the routine analysis of water and sewage. Determinations were made for pH, oxygen, carbon dioxide, calcium carbonate, ammonia, nitrite, nitrate, phosphate and iron.

Temperature records were obtained by a thermophone (Electrical Resistance Thermometer, Foxboro Manufacturing Company).

RESULTS

Flathead Lake

The temperatures of the water at the deep station, YB-D, taken at 1 m intervals, revealed no distinct thermocline but rather a steady decrease with increasing depth. These temperatures (Fig. 1) are typical of those recorded at other times of sampling. The record is complete to a depth of 97 m, the limit of the cable length.

A comparison of 1953 and 1954 results for the chemical analyses at the deep station, YB-D, shows only minor variations (Table I). The pH of the water was above 7.0 and usually near 8.0. The samples from Polson Bay (PB) were the most alkaline. Oxygen was high in all samples, averaging 10 ppm. At 106 m, YB-D, oxygen was 11 ppm. The concentration of oxygen increased with depth. No water samples from Flathead Lake showed an oxygen deficiency, another indication that Flathead Lake has no distinct thermocline. Sampling was limited to June, July and August; perhaps monthly sampling would reveal a thermocline.

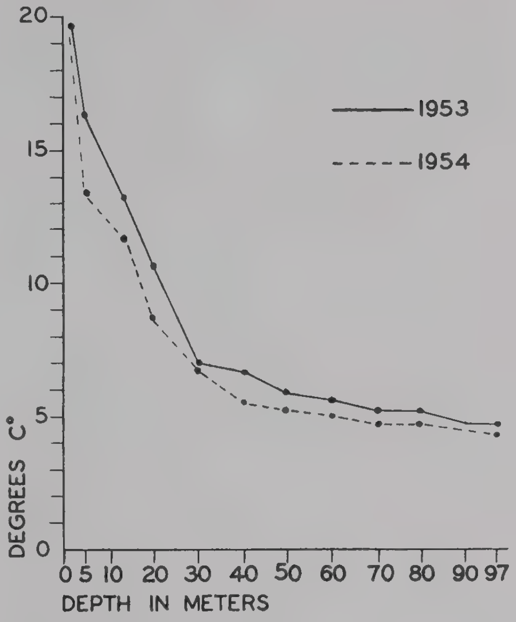

FIG. 1. Temperatures of water, deep station, Yellow Bay, Flathead Lake, Montana, July 11, 1953 and July 6, 1954.

There was no free carbon dioxide in any sample. The carbonates, as determined by the phenolphthalein and methyl orange titrations, indicated significant amounts of carbon dioxide present in this form. Flathead Delta (FD) contained the lowest concentration of carbonates. In the other 3 areas the concentrations were similar and did not change greatly with increasing depth. Traces of ammonia were present in all samples from Big Arm Bay (BA) and Flathead Delta (FD). The only positive test for nitrite was from the Big Arm Bay surface sample, indicating that nitrite is generally absent. Nitrate in small amounts often was present in water samples from all stations of the lake. It was present generally in surface samples, in those near the surface and in those taken near the bottom. In the middle depths of the deep station, YB-D, nitrate was absent. Phosphates sometimes were present (Table I), but their occurrence was erratic and occasional. Iron was present in small amounts on occasion as indicated by comparison of records in Table I. Occasionally significant amounts were found, as in 1954 at the 5 m level of the deep station. The significance of the iron in this sample was not apparent although it seemed unlikely that its presence was due to contamination of the sample. As

TABLE I. Chemical analysis of water, Flathead and Rogers Lakes, Montana

Station	Date	Temperature C°	Depth Meters	pH	Dissolved oxygen ppm	CO_2 ppm	Phenolphthalein ppm*	M. O. ppm**	NH_3 ppm	NO_2 ppm	NO_3 ppm	PO_4 ppm	Fe ppm
YB-D...	7-11-53	19.7	0.0	8.2	10.0	0	1.7	48.9	0.00	0.00	0.02	0.40	0.00
		—	0.5	8.2	10.0	0	2.9	26.9	0.00	0.00	0.02	0.20	0.00
		19.4	1.0	8.2	10.0	0	3.8	10.2	0.00	0.00	0.02	0.40	0.00
		16.4	5.0	8.2	11.0	0	3.7	46.3	0.00	0.00	0.01	0.20	0.00
		13.3	10.0	8.2	11.0	0	3.1	56.8	0.00	0.00	0.00	0.20	0.00
		10.6	20.0	8.0	11.0	0	2.6	51.4	0.00	0.00	0.00	0.20	0.00
		6.7	40.0	8.0	11.0	0	3.8	39.3	0.00	0.00	0.00	0.00	0.00
		5.3	80.0	8.0	11.0	0	2.7	57.6	0.00	0.00	0.00	0.00	0.00
		—	100.0	8.0	11.0	0	2.5	80.2	0.00	0.00	0.00	0.00	0.00
	7- 6-54	19.7	0.0	8.3	10.0	0	4.0	83.0	0.01	0.00	0.03	0.00	0.05
		17.4	1.0	7.9	10.0	0	3.0	85.0	0.01	0.00	0.00	0.00	0.01
		—	1.69	8.1	10.0	0	2.0	83.0	0.00	0.00	0.00	0.00	0.05
		13.4	5.0	8.1	11.0	0	2.0	86.0	0.00	0.00	0.00	0.00	1.2
		11.6	10.0	7.0	11.0	0	1.0	78.0	0.00	0.00	0.00	0.00	0.05
		8.6	20.0	7.1	11.0	0	1.0	84.0	0.00	0.00	0.00	0.00	0.03
		5.5	40.0	8.1	12.0	0	1.0	83.0	0.00	0.00	0.00	0.00	0.09
		4.7	80.0	8.1	12.0	0	1.0	77.0	0.00	0.00	0.00	0.00	0.08
		—	106.0	8.1	11.0	0	1.0	77.0	0.00	0.00	0.02	0.00	0.05
FD......	7-11-54	10.0	0.0	7.8	10.5	0	0.0	73.5	0.01	0.00	0.04	0.00	0.02
		9.0	1.0	8.1	10.5	0	0.0	70.2	0.01	0.00	0.03	0.00	0.1
		10.0	1.69	7.6	10.5	0	0.0	68.8	0.01	0.00	0.03	0.00	0.02
		11.0	5.0	7.8	10.0	0	0.0	69.5	0.01	0.00	0.04	0.00	0.01
		10.0	9.5	7.8	10.0	0	0.0	70.5	0.01	0.00	0.03	0.00	0.01
BA......	7- 1-54	15.0	0.0	8.3	10.5	0	3.5	80.0	0.01	0.0005	0.02	0.00	0.1
		15.5	1.0	8.1	10.5	0	3.5	80.2	0.01	0.00	0.03	0.00	Trace
		15.5	1.69	7.7	10.0	0	0.5	80.0	0.01	0.00	0.03	0.00	Trace
		14.0	5.0	8.2	11.0	0	3.6	80.0	0.01	0.00	0.03	0.00	0.3
		13.0	10.0	7.8	11.0	0	1.5	80.0	0.01	0.00	0.03	0.00	Trace
		9.0	17.0	7.9	11.0	0	2.0	81.5	0.01	0.00	0.03	0.00	Trace
PB......	6-29-54	15.0	0.0	8.3	10.0	0	2.2	85.7	0.01	0.00	0.025	0.00	0.00
		16.0	1.0	8.3	10.0	0	2.0	83.9	0.00	0.00	0.05	0.00	0.00
		16.0	2.0	8.3	10.0	0	2.1	83.0	0.00	0.00	0.03	0.00	0.00
Rogers #1	7-16-54	22.5	0.0	7.3	5.5	—	0.0	122.0	0.07	0.00	0.12	0.00	0.02
Rogers #2	7-16-54	23.0	0.0	8.5	8.7	0	4.6	108.0	0.03	0.00	0.04	0.00	0.00
		21.7	1.5	8.5	8.9	0	4.1	109.0	0.02	0.00	0.05	0.00	0.00
Rogers #3	7-13-54	19.8	0.0	8.3	8.5	—	4.9	110.1	0.02	0.00	0.07	0.00	0.00
		20.1	1.0	8.5	8.5	—	5.0	111.2	0.01	0.00	0.08	0.00	0.00
		20.1	2.0	8.4	8.4	—	6.8	109.1	0.01	0.00	0.07	0.00	0.00
		19.8	4.0	8.5	10.0	—	5.0	112.3	0.01	0.00	0.04	0.00	0.00
		20.0	5.0	8.3	9.0	—	5.7	110.0	0.02	0.00	0.04	0.00	0.00

* ppm of carbonate, Phenolphthalein titration.
** ppm of carbonate, Methyl Orange titration.

with the phosphates, the presence of iron was erratic.

A tabulation of bacterial counts per cc of water at the various sampling levels of the deep station (YB-D) in 1953 is given in Table II. The count was low at all levels. Most samples below the surface had low counts, sometimes being practically bacteria free. The highest count was obtained at the 10 m level; the next highest at the surface.

In 1954 the counts per cc at the selected levels of the deep station, YB-D, were of the same order as those of 1953, but the highest count was at 40 m (Table II). The highest number of bacteria per sample was from Flathead Delta (FD). When this sample was taken there was a great deal of turbulence because the North Fork of the Flathead River was in spring flood. The water was turbid with silt being carried into the lake. The high counts, therefore, may have been due to organisms in transport with silt. The numbers of bacteria at different levels of Big Arm Bay (BA) and Polson Bay (PB) were lower than those of the delta, FD, and the same as those of the deep station, YB-D, with the exception of the surface sample. The figures in Table II reveal that the largest numbers of bacteria were found at the surface and in the bottom layer of water.

TABLE II. Vertical distribution of microorganisms in Flathead and Rogers Lakes, Montana, 1953 and 1954

Station	Date	Depth Meters	No. bacteria per cc	Total % chromogens	No. fungi per cc
YB-D..........	7-11-53	0.0	26.0	69.0	2.0
		0.5	3.0	53.0	0.0
		1.0	10.0	50.0	0.0
		1.69	18.0	47.0	4.0
		5.0	5.4	27.0	6.0
		10.0	31.0	51.0	0.0
		20.0	10.0	36.0	2.0
		40.0	20.0	70.0	1.0
		80.0	—	—	4.0
		100.0	6.4	34.0	4.0
		*Mud	0.780	14.0	0.0016
YB-D..........	7- 7-54	0.0	16.0	56.0	3.6
		0.1	2.0	55.0	10.0
		1.0	9.0	77.0	1.4
		1.69	18.0	76.0	1.4
		5.0	3.5	57.0	1.2
		10.0	25.0	94.0	1.0
		20.0	10.0	55.0	1.2
		40.0	60.0	80.0	10.0
		80.0	26.8	85.0	8.0
		100.0	22.0	50.0	1.0
		*Mud	0.79	14.0	0.0014
FD............	7-11-54	0.0	940.0	56.0	26.0
		0.1	87.0	90.0	38.0
		1.0	221.0	60.0	56.0
		1.69	95.0	62.0	46.0
		5.0	150.0	61.0	40.0
		8.0	318.0	57.0	44.0
		*Mud	11.7	56.0	0.038
BA............	7- 1-54	0.0	350.0	83.0	20.0
		0.1	2.3	78.0	38.0
		1.0	4.6	33.0	28.0
		1.69	9.0	89.0	36.0
		5.0	4.0	50.0	36.0
		10.0	7.0	35.0	44.0
		17.0	17.0	43.0	36.0
		*Mud	0.259	42.0	0.0042
PB............	6-29-54	0.0	750.0	77.0	36.0
		0.1	13.0	58.0	32.0
		1.0	19.0	72.0	24.0
		2.0	54.0	86.0	42.0
		*Mud	4.6	67.0	0.0044
Rogers #1.......	7-16-54	0.0	2,300.0	51.0	460.0
		0.5	75.0	49.0	520.0
		*Mud	1.7	42.0	0.540
Rogers #2.......	7-16-54	0.0	820.0	55.0	780.0
		1.5	60.0	47.0	640.0
		*Mud	0.198	66.0	0.760
Rogers #3.......	7-13-54	0.0	1,090.0	29.0	26.0
		0.1	79.0	68.0	30.0
		1.0	275.0	88.0	26.0
		2.0	121.0	91.0	12.0
		4.0	80.0	76.0	26.0
		4.5	150.0	85.0	22.0
		*Mud	0.0427	18.0	0.012
Rogers #4.......	7-16-54	0.0	13,700.0	74.0	360.0
		*Mud	17.1	46.0	0.40

* Numbers in mud as millions per gm wet weight.

Between the surface and bottom there were few bacteria. At the deep station the relatively high counts at 40 m may be due to flow of water at this depth. The nature of the currents at this station, YB-D, is not understood, but observations by various investigators indicate that there may be strong, deep currents there. If so, these might bring in a population which does not mix with water above or below.

In 1954 mud and water samples were collected from each of the stations at the same time. The numbers of bacteria per gram of mud are given in Table II. These numbers are considerably smaller than those reported in the preliminary survey of 1951. If, however, the counts are ranked in descending order from the largest figure, the ranking is of the same order as that recorded previously by Potter and Baker (1956).

The percentage of chromogens in the water and mud of Flathead Lake was usually high (Table III). The chromogen population was inversely proportionate to the depth of the bottom mud. Usually the chromogen percentage of water exceeded that of the mud. The predominant group was yellow-orange, ranging from light yellow to deep orange. No attempt was made to subdivide the group into separate categories. True red organisms were found in surface samples from the deep station, YB-D. Pink organisms occurred in samples from all stations but were dominant in the surface samples from Big Arm Bay. The percentage of pink organisms was often higher in surface samples. Aside from the percentages of red and pink organisms there was no indication of vertical distribution patterns among the various groups or for the total percentages of chromogens.

Microscopic examination of the 1953 YB-D samples revealed that Gram negative organisms were most numerous at the surface and least numerous at the bottom (Table IV). This was true also for the 1954 deep station samples and for all stations except Flathead Delta. With the exception of Polson Bay there were fewer Gram negative organisms in the mud than in the water above. The majority of Gram negative organisms were pleomorphic rods. Many of the Gram positive rods also were pleomorphic. There were significant numbers of cocci and spore-formers in both water and mud samples. A small number of yeasts was obtained from what appeared to be typical bacterial colonies. This does not represent the true incidence of yeasts, but only those which form colonies resembling bacterial colonies.

Quantitative study of the fungus population in vertical distribution in Flathead Lake was carried on simultaneously with the bacterial analyses of 1953 and 1954. The methods and materials were those used in the bacterial studies. Counts of fungi in vertical distribution at the 4 stations were made (Table II). Qualitative analysis of the

TABLE III. Percentages of chromogens in bacterial populations of Flathead and Rogers Lakes, Montana, 1954

Station	Date	Depth Meters	% Red	% Yellow-orange	% Pink	% Algae
YB-D	7- 7-54	0.0	3	36	17	0
		0.1	0	55	0	0
		1.0	0	66	11	0
		1.69	0	75	1	0
		5.0	0	57	0	0
		10.0	0	94	0	0
		20.0	0	50	5	0
		40.0	0	80	0	0
		80.0	0	85	0	0
		100.0	0	50	0	0
		Mud	0	14	0	0
FD	7-11-54	0.0	0	56	0	0
		0.1	0	81	9	0
		1.0	0	59	1	0
		1.69	0	60	2	0
		5.0	0	59	2	0
		10.0	0	55	2	0
		Mud	0	55	1	0
BA	7- 1-54	0.0	0	29	54	0
		0.1	0	65	13	0
		1.0	0	33	0	0
		1.69	0	89	0	0
		5.0	0	50	0	0
		10.0	0	35	0	0
		17.0	0	41	2	0
		Mud	0	41	1	0
PB	6-29-54	0.0	0	60	17	0
		0.5	0	58	0	0
		1.0	0	72	0	0
		2.0	0	73	13	0
		Mud	0	63	4	0
Rogers #1	7-16-54	0.0	0	46	5	0
		0.5	0	41	2	6
		Mud	0	38	2	2
Rogers #2	7-16-54	0.0	0	50	5	0
		1.5	0	45	2	0
		Mud	0	20	4	42
Rogers #3	7-13-54	0.0	0	29	0	0
		0.1	0	68	0	0
		1.0	0	88	0	0
		2.0	0	91	0	0
		4.0	0	76	0	0
		4.5	0	84	1	0
		Mud	0	13	1.3	4
Rogers #4	7-16-54	0.0	0	69	5	0
		Mud	0	39	7	0

counts by species was made in addition. Ninety-eight species of 62 genera were identified from Flathead Lake samples. Forty-two of these genera were represented by a single species. For the remaining 20 genera species representation was of the following order: 1 genus, *Penicillium,* 13 species, but 7 of these were single isolations; 3 genera with 4 species each; 5 genera with 3 species each; and 11 genera with 2 species each. The vertical distribution of the fungi identified is summarized in Table V. Counts and a summary of the fungi identified from the associated bottom muds are included in Tables II and V.

The numbers of fungi in the water of the deep station, YB-D, are too low to be quantitatively significant. The occurrence of species is more interesting. Counts for the bottom muds exceeded those of the water and usually the number of species occurring in the mud was in excess of the number in water. Numbers from the delta, FD, Big Arm Bay and Polson Bay, showed a definite increase in both water and mud over the numbers from the deep station, yet the number of species isolated from the deep station water samples was much greater. Only Flathead Delta approximated the deep station in the number of species isolated from both mud and water. None of the counts from the 4 stations gave any indication of a distribution pattern in the water from surface to bottom. Only 1 fungus, *Hormodendrum hordei,* occurred at all 4 levels sampled in Polson Bay. Two fungi, *H. hordei* and a species of *Fusarium* (recorded as #4), were isolated from all depths sampled at the deep station in 1954. *Fusarium* #4 was isolated from 6 of the 7 water samples taken at Big Arm Bay in 1954. *Geotrichum candidum* appeared in 5 of the 6 Flathead Delta water samples. These 3 fungi were ubiquitous in both water and mud samples at all stations with the following exceptions: *G. candidum* not recorded for Polson Bay or Big Arm Bay mud; *H. hordei* not present in Flathead Delta mud; and *Fusarium* #4 absent in Polson Bay mud. All 3 fungi have been isolated in previous or successive years from the muds of these locations (Baker unpublished data). Fungus species common to mud and water represented 20% or more of the total populations for all stations. Specifically these percentages were: YB-D, 1953, 54%; YB-D, 1954, 36%; FD, 29%; BA, 20%; and PB, 20%.

Rogers Lake

The results of the chemical analysis on water samples from Rogers Lake are summarized in Table I. There was little variation in the temperature of the water, but Rogers Lake is only slightly more than 5 m at its greatest depth. The pH of the water and the concentration of the carbonates generally were higher than for Flathead Lake. Significant amounts of ammonia and nitrate were present in all samples. Nitrate occurred in excess of ammonia. No significant amounts of nitrite, phosphate or carbon dioxide were found and only once was a positive test for iron obtained. The oxygen concentration was lower than that of Flathead Lake. The lowest oxygen concentration was at Station 1 which lies between a bed of *Scirpus* and a mat of *Carex.*

Bacterial populations are recorded in Table II. The inlet spring had a high number of bacteria.

TABLE IV. Morphology and Gram reaction of bacteria from Flathead and Rogers Lakes, Montana, 1953 and 1954

Station, Date	Depth, Meters	% Gram negative pleomorphic rods	% Gram negative rods	% Gram negative cocci	% Gram positive pleomorphic rods	% Gram positive rods	% Gram positive cocci	% Gram positive spore-formers	% yeasts	Total % Gram negative organisms
YB-D 1953	0.0	65	18	3	0	0	5	8	—	86
	0.5	35	20	5	0	5	30	0	—	60
	1.0	30	40	0	5	15	5	5	—	55
	10.0	45	33	6	0	1	13	0	—	84
	20.0	20	20	5	10	20	10	0	—	45
	40.0	35	15	5	10	0	25	0	—	55
	100.0	25	10	0	20	15	10	5	—	35
YB-D 1954	0.0	54	26	6	2	6	0	6	0	86
	1.0	39	38	2	12	2	3	3	0	79
	1.69	41	30	1	7	14	4	2	0	72
	10.0	31	26	14	11	0	11	4	2	71
	20.0	22	27	5	22	6	12	6	0	54
	40.0	42	20	5	12	6	14	0	0	67
	80.0	9	20	10	4	11	40	4	1	39
	105.0	20	53	1	3	6	13	2	0	74
	Mud	8	28	2	2	3	5	50	2	38
FD 1954	0.0	27	51	0	4	4	7	0	0	78
	0.1	40	46	6	3	0	5	0	0	92
	1.0	47	40	3	5	0	2	0	0	92
	1.69	32	58	5	5	0	0	0	0	95
	5.0	20	55	8	3	1	7	5	0	83
	9.5	40	43	10	0	1	1	5	0	93
	Mud	34	30	10	8	2	15	0	0	74
BA 1954	0.0	90	5	0	1	0	4	0	0	95
	17.0	70	10	1	7	0	4	6	1	81
	Mud	61	6	2	10	0	6	14	0	69
PB 1954	0.0	61	20	8	2	3	2	2	0	89
	0.1	44	25	7	0	0	5	15	3	75
	1.0	56	13	6	0	0	16	6	2	75
	2.0	58	7	12	1	1	11	10	0	77
	Mud	66	18	10	2	2	2	0	0	94
Rogers Lake, Station #3, 1954	0.0	57	37	0	3	2	0	0	0	94
	0.1	55	25	5	4	4	6	0	0	85
	1.0	57	16	11	0	0	10	0	5	84
	2.0	46	41	0	5	0	7	0	0	87
	4.0	23	16	0	38	5	10	3	4	39
	4.5	33	0	0	53	3	10	0	1	33
	Mud	0	2	0	21	31	10	35	0	2

The largest populations were in the surface samples. Numbers of bacteria per cc dropped rapidly with depth. At the deepest station all samples below the surface contained significantly smaller populations than the surface samples, but the decrease in population was not consistent with increasing depth. In the mud the number of bacteria per gm was smaller than that recorded in 1951 by Potter and Baker (1956) for Station 4, the spring and for Station 3, the open lake. The population at Station 3 was of the same magnitude as that reported in 1951 (Potter and Baker 1956).

Percentages of chromogens in Rogers Lake are shown in Table III. These were generally high, with the yellow-orange group predominant. Pink organisms were occasionally present, notably in surface samples. The percentage of chromogens in mud samples usually was lower than in water and generally decreased with increasing depth. Algae were present in significant numbers in mud samples from the open lake. At Station 2, on the east side of the *Scirpus* bed, algae constituted the largest group of chromogens: 42%. A significant number of algal colonies was found in the water sample taken immediately above the mud at Station 1.

Investigation of the morphology and Gram reaction of the bacteria from Rogers Lake showed a distinct decrease in Gram negative organisms from the surface to the mud (Table IV). The mud contained significantly few Gram negative rods. Many of the Gram negative and Gram positive rods were pleomorphic. A few cocci and yeasts were found. The water had a few spore-

TABLE V. Vertical distribution of fungus species: Flathead Lake, Montana, 1953 and 1954; Rogers Lake, Montana, 1954. (Numbers based on all dilutions plated)

Depth Meters	NUMBER OF SPECIES ISOLATED:								
	YB-D, '53	YB-D, '54	FD	BA	PB	Rogers #1	Rogers #2	Rogers #3	Rogers "4
0.0	5	10	19	7	13	11	10	4	3
0.1	1	10	14	9	7	—	—	9	—
0.5	0	—	—	—	—	10	—	—	—
1.0	0	5	10	8	8	—	—	9	—
1.5	—	—	—	—	—	—	7	0	—
1.69	5	10	14	6	—	—	—	—	—
2.0	—	—	—	—	4	—	—	3	—
4.0	—	—	—	—	—	—	—	10	—
4.5	—	—	—	—	—	—	—	—	—
5.0	3	8	13	5	—	—	—	—	—
8.5	—	—	10	—	—	—	—	—	—
10.0	0	9	—	7	—	—	—	—	—
17.0	—	—	—	6	—	—	—	—	—
20.0	3	11	—	—	—	—	—	—	—
40.0	4	12	—	—	—	—	—	—	—
80.0	1	12	—	—	—	—	—	—	—
100.0	4	8	—	—	—	—	—	—	—
Mud	26	23	22	12	8	9	11	10	7

formers but a significantly large number occurred in the gelatinous ooze which constitutes the bottom at Station 3 (Potter and Baker 1956).

Analysis of the fungus populations in Rogers Lake in 1954 was made on the samples used for bacterial studies. The quantitative counts for the 4 stations are recorded in Table II. Station 3, the open lake, had a population markedly lower than that of the other 3 locations. There was a ten-fold difference between the count of the open lake and the counts of the other areas. Between water and mud counts there was consistently an approximate thousand-fold difference. At no single level was the population significantly different for any of the stations studied. Qualitatively, 36 species of fungi representing 25 genera, were identified from these stations and their associated bottom muds. Twenty of these species occurred in the bottom samples; 4 were limited to the bottom mud. Analysis of species by location revealed 20 species at Station 1, between the *Scirpus* bed and *Carex* mat; 17 species at Station 2, the east side of the *Scirpus* bed; 19 species at Station 3, the open lake; and 8 species at Station 4, the spring inlet. The penultimate number of species was isolated from the open lake although the count there was lower. Only *Cladosporium elatum* was found in the water of all 4 stations. *Geotrichum candidum* and *Cladosporium herbarum* were common to the water of Stations 1, 2 and 3 and both were common to the bottom mud of all 4 locations.

DISCUSSION

The chemical analysis of the water of Flathead Lake showed that it was usually slightly alkaline. The water was rich in carbonates and oxygen at all depths. Oxygen distribution in Flathead Lake has been discussed by Young (1935). The findings reported here are in keeping with his observations and those of subsequent investigators. Nitrite was consistently absent except for a trace recorded once from the surface water of Big Arm Bay. Ammonia and nitrate occurred in small quantities sporadically at all stations but not necessarily at all depths. Nitrate levels exceeded those of ammonia. Phosphates and iron were present, iron appearing more commonly than phosphates. No distribution pattern is evident for any of these constituents. Analysis over a period of time would be valuable in determining the possibility of seasonal variation in the chemical composition of Flathead Lake water. The results indicated that there was no true thermocline or chemical stratification, unless the lack of nitrate at the intermediate levels of the deep station (YB-D) should be interpreted as stratification.

The largest populations of bacteria in Flathead Lake were at the surface, followed in number by those of the bottom layers. In 1953 and 1954 relatively large populations were found at the 40 m level of the deep station. Little is known about the currents in Flathead Lake, but strong ones appear to be present at the lower levels of the deep station. Such movement of water could be transporting materials and microorganisms through the area without mixing with the surrounding water layers. At the time of sampling in the delta region, the Flathead River was in flood, carrying visible quantities of silt into the lake. The high counts probably represent a large microbial population carried by the silt. Taylor (1940) and Fred, Wilson and Davenport (1924) have reported that many organisms so transported into a lake by streams soon disappear. This would account for sporadic increases in the population. The number of microorganisms carried in by a stream will depend, naturally, on the character of that stream and its watershed. Most of the country drained by the Flathead River is uninhabited and little of the drainage area is cultivated. The chief source of the water is in the mountains of Glacier National Park. The South Fork also flows from mountains and through uninhabited country. Such rivers would not be so heavily contaminated as those which flow through well populated and cultivated lands. The largest microbial populations in Flathead Lake are not necessarily found at the delta (Potter and Baker 1956). The high counts of 1954 are an indication of considerable seasonal variation correlated with the volume of water entering the lake.

Counts of microorganisms in the water of Flathead Lake are usually low, but the numbers presented here are generally lower than those reported earlier by Potter and Baker (1956). Neither do the results substantiate the findings of Graham and Young (1934) or Potter and Baker (1956) that the 5½ ft depth had the greatest population, since the surface population exceeded all others. Within a depth of 0.1 m the population was greatly decreased. As there was little change in the chemical composition of the water from surface to bottom, the high surface count would appear due to other factors. Air contamination, the trapping of organisms at the interface of air and water, or stimulation from organic chemicals occurring only at the surface, might be possible explanations.

Comparison of the microbial populations of the mud shows lower numbers for 1954 than those reported for 1951 (Potter and Baker 1956). The methods used in obtaining and handling the samples were the same in both years, so there is no obvious reason for the decrease. Seasonal variation may characterize the bottom mud population as well as that of the water.

It was not possible to demonstrate vertical distribution patterns by analysis of the percentage of chromogens. Figures for red organisms were hardly significant. Individual groups of other chromogens did show patterns of distribution, particularly the pink group. These pink organisms have always been isolated from Big Arm Bay in significant numbers, which suggests that they are autochthonous for that area. The fact that the pink organisms were more plentiful in surface samples indicated that they are typically surface inhabitants. This further suggests that various areas and depths of the lake have representative populations, even endemic ones. The chemical and physical characteristics, alone or in combination, of the surface may differ from area to area although the analyses showed only slight differences in chemical constituents present in the 4 surface areas. Undoubtedly, too, the organic content of the water is important in determining the microbial make-up of a given area.

A study of the morphology and the Gram reactions of the bacteria showed that the majority of organisms were Gram negative. Predominant in that group were pleomorphic rods. Usually there were more Gram negative organisms at the surface than at other water levels. The lowest numbers were in the mud. Morphological characteristics determined from plates of sodium caseinate agar after 14 to 21 days' incubation may not be comparable to those from young cultures on more suitable media. When subcultured on other media, however, many cultures of Gram negative pleomorphic rods retained their characteristics. An initial incubation period of this length was necessary to obtain a maximum count. Numerous comparative studies with a variety of media have shown repeatedly that sodium caseinate agar plates produce the highest counts and the most diversified populations (Potter and Baker, unpublished data).

Analysis of the morphological results shows a vertical distribution of bacteria which is similar for both Flathead and Rogers Lakes. The Gram negative organisms are more common near the surface than below it. The distribution of some chromogenic bacteria also indicates a vertical distribution. There are bacteria at all levels of the water, although the numbers vary from level to level. Some organisms, such as the red ones in Flathead Lake, appear to occur primarily at the surface.

When the numbers, chromogenic and morphological characteristics of the bacteria in the mud were compared to those in the water, there appeared to be two distinct populations: one for mud and one for water. There were a few to many bacteria common to both regions, but the total population seemed to be distinct for each.

Surface water and bottom mud had the largest populations. Those at the surface may represent survivors from the air, floating objects and surface run-off. The mud population may be constituted by those which have settled to the bottom. But from the evidence presented here it appears that the two populations have little in common. This suggests that there is an autochthonous microbial population for water and another for mud.

Study of the fungus population of Flathead Lake obtained at 4 stations by using selected sampling levels in vertical distribution, revealed no significant population at any given level from surface to bottom. There was no evidence that 5½ ft represented a level of maximum fungus population, as suggested by Graham and Young (1934) for bacterial numbers. The fungus counts in the water at the 4 sampling localities were significant qualitatively but not quantitatively. The associated bottom mud samples did have quantitatively measurable fungus populations. The species common to mud and water represented a sizeable percentage of the species isolated from the water. The percentage of fungus species common to mud and water at the deep station (YB-D) was larger than the percentages obtained at all other stations. It correlated with the higher number of species identified from the deep station isolates. Two fungi were represented at all the water levels of YB-D: *Fusarium* #4 and *Hormodendrum hordei*. Both species occurred at all but one of the levels sampled at Big Arm Bay. This frequency is consistent with the known frequency of representatives of these genera. Both *Fusarium* and *Hormodendrum* species are of wide occurrence in soil and aquatic environments (Weston 1941, Warcup 1951, Kao 1952, Farrow 1954, and Gilman 1957).

With the exception of the 1953 deep station mud samples, the number of species found was lower than the number isolated from corresponding water samples. This could mean that the persistent population of the lake is a selected one. It has not been determined whether the organisms constituting the fungus population occur as spores, as viable mycelium or actual growing colonies. Some experimental evidence suggests that selected species are in an active growing condition in the water (Baker, unpublished data).

A study of vertical distribution is important in obtaining as thorough an understanding of a given aquatic environment as possible. The literature on lake populations offers no specific data for fungi, so the results presented here can be interpreted only at their face value. Results indicate that qualitatively there is a significant fungus population present in Flathead Lake at all times, in all locations and at all depths. The number of isolates was in consistent range for the 4 locations sampled and for most stations at all depths. The absence of fungi at a given water level was rare enough to be interpreted as a characteristic of random sampling, coupled with variations in the physical and chemical nature of the lake. For example, although there were no fungi in the 10 m sample taken from the deep station in 1953, fungi were isolated at that depth in 1954.

The fungi in the bottom mud are regarded as a persistent population. This is the largest population numerically and the species comprising it are commonly represented annually (Baker, unpublished data). Subsequent experimental work has shown the persistence of these species over long periods and under conditions both similar and dissimilar to their isolation environment (Baker, unpublished data).

The chemical studies of Rogers Lake water showed little variation in chemical constitution from station to station. Ammonia and nitrates were available in solution but not phosphate. Again it would be advantageous to have sampling data distributed throughout the year to disclose possible nitrogen and phosphorus cycles. The tests performed did not consider the nature or amounts of organic chemicals in the water, but the consistent presence of ammonia and nitrate indicates that Rogers Lake is richer than Flathead Lake. This agrees with the usual designation of Rogers Lake as eutrophic and Flathead Lake as oligotrophic.

In both lakes the surface samples often had the largest microbial populations. Surface counts from Rogers Lake were higher than those from Flathead Lake. In both lakes the inlet areas had the highest counts for the entire lake. A comparison of counts and characteristics of the organisms in the mud and in the water contiguous to the mud indicated little migration of bacteria from mud to water.

A high percentage of the organisms in Rogers Lake was composed of chromogens. The yellow-orange group was the largest as it was in the Flathead Lake samples. In both lakes the pink chromogens were most numerous at the surface or near it. Although the two lakes are very different in physical characters and show some biological differences as well (Lauff 1953, Brunson and Nelson 1952, Potter and Baker 1956), there did not appear to be a striking difference in either their microbial populations or their chemical make-up. Rogers Lake water has a lower concentration of oxygen, a higher concentration of carbonates and a more consistent presence of ammonia and nitrate than Flathead Lake. This could account for the larger surface counts from Rogers Lake in 1954 in comparison with surface counts that year in Flathead Lake. This difference was less noticeable in 1951.

Significant numbers of algal colonies grew on the sodium caseinate plates from samples of Rogers Lake. Occasionally algal colonies have been observed in material from Flathead Lake but never in the numbers represented in Rogers Lake. In fact, for some samples the algal colonies constituted a large proportion of the total population (Table II).

In both lakes there was a sharp decrease in the bacterial population from surface to just below the surface. There was no consistent increase or decrease in populations at intermediate depths but a significant increase at levels just above the mud. The mud at all stations had a much larger bacterial population than the water just above it. The migration of bacteria from surface down or from mud up did not appear to be great. The smaller number of chromogens in mud samples indicated that the natural populations of mud and water are different although some organisms may be common to both. The morphological characteristics of the bacteria further supported the concept of two autochthonous populations, one for mud and one for water.

The higher fungus counts from Stations 1, 2 and 4 of Rogers Lake compared with those of Station 3, the open lake, probably mean associations with marginal plant life. The low count for mud at Station 3 probably correlates with the type of bottom (Potter and Baker 1956). The high number of species in the open lake corresponds to similar findings for Flathead Lake. The number of species from the open lake samples, Station 3, compared favorably with numbers of species from the other stations. This indicates that the higher counts represented repeated isolations of the same fungi. The marginal shallow areas probably offered more favorable locations for growth and sporulation which would be reflected in the counts obtained, but not in the number of species present (Hack 1957).

SUMMARY

1. Vertical distribution of the bacteria and fungi in Flathead and Rogers Lakes, Montana, was investigated and chemical analysis made of the water from the sampling locations. The two lakes were compared biologically and chemically.

2. The water of Flathead Lake was alkaline, ranging from pH 7.0 to 8.3. The pH may vary with depth at a given station but often was the same at all depths. The pH of Rogers Lake water ranged from 7.3 to 8.5.

3. There was no oxygen deficiency in Flathead Lake even at a depth of 107 m. There was less oxygen available in Rogers Lake. No free CO_2 occurred in either lake but significant amounts of CO_2 as carbonates were present in Flathead Lake and higher amounts in Rogers Lake.

4. Ammonia was present at least in small amounts at all areas in Flathead Lake but not at all depths of a given station. Larger amounts were more consistently present in Rogers Lake. Nitrite was absent in both lakes except for the surface of Big Arm Bay in Flathead Lake. Nitrate occurred in varying amounts at all stations of both lakes. Iron and phosphates occurred sporadically in Flathead Lake. No phosphate was found in Rogers Lake and iron was found only once.

5. The highest counts of bacteria were usually in surface and bottom waters of Flathead Lake. The vertical pattern is less definitive for Rogers Lake since it is at most 4.5 m deep, but the surface samples had consistently and conspicuously the largest populations. In both lakes the associated bottom mud populations were many times larger than any water populations reported. Variations in counts from the water could be correlated with seasonal conditions in Flathead Lake.

6. Chromogens were representative of the water populations in both lakes. Some particular chromogens were endemic to a given area. Algae were found in large numbers in the mud of one Rogers Lake sampling area.

7. The dominant bacterial types in Flathead Lake samples were Gram negative rods, most of which were pleomorphic. Many Gram positive rods were also pleomorphic. Cocci, spore-formers and yeasts occurred at times in significant numbers in both water and mud. The occurrence of these microorganisms in Rogers Lake was similar to that in Flathead Lake. Gram negative rods occurred in a lower order of frequency in bottom mud samples from both lakes.

8. Fungi were present in water and mud of both lakes. Water counts were not quantitatively reliable. The greatest variety of species occurred at the deep station of Flathead Lake. There was neither a vertical distribution pattern nor a level of maximum concentration. From 20-54% of the fungus species in Flathead Lake were common to both mud and water. In Flathead Lake the open lake had the greatest diversity of species. The findings for the open station in Rogers Lake were comparable. In Rogers Lake 41% of the fungi were common to water and mud.

9. At total of 98 species of fungi was identified from Flathead Lake and 36 species from Rogers Lake. Of these 98 species 25 were common to both lakes, 73 occurred in Flathead Lake and 11 were limited to Rogers Lake.

10. The data obtained from the water and bottom mud samples suggest that the bacterial populations of the two lakes are autochthonous for the two types of habitat, water and mud.

11. The relatively high percentages of fungi common to water and mud of a given location do not support the idea of a distinct population for each of these two habitats.

12. The population counts and species analyses

of fungi support the contention that there is a persistent fungus population in each of these lakes. The greater number of species found in Flathead Lake is in keeping with its larger size, if not with the usual oligotrophic designation for this lake. If size of population correlates with eutrophism and oligotrophism, Rogers Lake should have a much larger fungus population than was found by these studies. It is suggested, therefore, that this limnological classification is not necessarily definitive for the occurrence of fungus species.

REFERENCES

Brunson, R. B. and H. E. Nelson. 1952. A limnological reconnaissance of three western Montana lakes. Proc. Montana Acad. Sci. **12**: 45-61.

Farrow, W. M. 1954. Tropical soil fungi. Mycol. **46**: 632-646.

Fred, E. B. and S. A. Waksman. 1928. Laboratory manual of general microbiology. McGraw-Hill Book Co., Inc., New York.

Fred, E. B., F. C. Wilson and A. Davenport. 1924. Distribution and significance of bateria in Lake Mendota. Ecology **5**: 322-339.

Gilman, Joseph C. 1957. A manual of soil fungi. Rev., 2nd ed. Ia. State College Press, Ames.

Graham, V. E. and R. T. Young. 1934. A bacteriological study of Flathead Lake, Montana. Ecology **15**: 101-109.

Hack, Judith E. 1957. The effect of spore germination and development on plate counts of fungi in soil. J. Gen. Microbiol. **17**: 625-630.

Kao, Chun-Juan. 1952. The influence of steam sterilization of the soil upon the distribution of microorganisms. Thesis, Vassar College, Poughkeepsie, N. Y.

Lauff, George. 1953. Contribution to the water chemistry and phytoplankton relationships of Rogers Lake, Montana. Proc. Montana Acad. Sci. **13**: 5-20.

Potter, Louise F. and Gladys E. Baker. 1956. The microbiology of Flathead and Rogers Lakes, Montana. I. Preliminary survey of the microbial populations. Ecology **37**: 351-355.

———, Donald Osterhoudt and Gladys E. Baker. 1958. A collecting bottle for the microbiological sampling of water. Ecology **39**: 363-364.

Soc. Amer. Bacteriologists. 1957. Manual of microbiological methods. 5th ed. McGraw-Hill Book Co., Inc., New York.

Taylor, C. B. 1940. Bacteriology of fresh water. I. Distribution of bacteria in English lakes. J. Hygiene **40**: 616-640.

Warcup, J. H. 1951. Effect of partial sterilization by steam or formalin on the fungus flora of an old forest nursery soil. Trans. Brit. Mycol. Soc. **34**: 519-532.

Welch, Paul S. 1952. Limnology. 2nd ed. McGraw-Hill Book Co., Inc., New York.

Weston, W. H. 1941. The role of aquatic fungi in hydrobiology. *In:* A symposium on hydrobiology. Univ. Wisc. Press, Madison.

Young, R. T. 1935. The life of Flathead Lake, Montana. Ecol. Monog. **5**: 91-163.

THE CHAPARRAL FORMATION OF SOUTHWESTERN OREGON, WITH CONSIDERATIONS OF ITS POSTGLACIAL HISTORY

LeRoy E. Detling
Museum of Natural History, University of Oregon, Eugene

INTRODUCTION

The term "chaparral" has been in popular use since the early settlement of western North America to designate a special type of scrub vegetation found, on this continent, largely in California. Usage has been so consistent and the application of the popular name so specific that the term has been adopted by ecologists. It designates a vegetation type made up of shrubs which tend to grow in dense stands. The individual plants possess relatively small, thick, heavily cutinized leaves, usually but not always evergreen, borne on rigid twigs and branches. They have extensive root systems. The community is normally dominated by one species, often in pure stand.

The chaparral of southwestern Oregon, like that of northern California, apparently may be either climax or subclimax. However, the floristic structure and ecological features of the community vary so little throughout its range that I use the term "formation" to apply to any stage of its development, even though obviously successional.

Few studies have been published dealing with the western American chaparral from the floristic standpoint. The outstanding investigation is that made by Cooper (1922) on the California broad-sclerophyll vegetation. In this work he deals extensively with the ecology of the chaparral community and the species comprising it. The published results of his California field studies do not specifically relate his findings to the Rogue River chaparral, and my observations in southwestern Oregon lead me to believe that this rather extensive, though more or less isolated, chaparral area needs further investigation. The fact that the flora of the Rogue Valley constitutes the northern outpost of the California flora gives promise of clarifying its relation to surrounding or overlapping

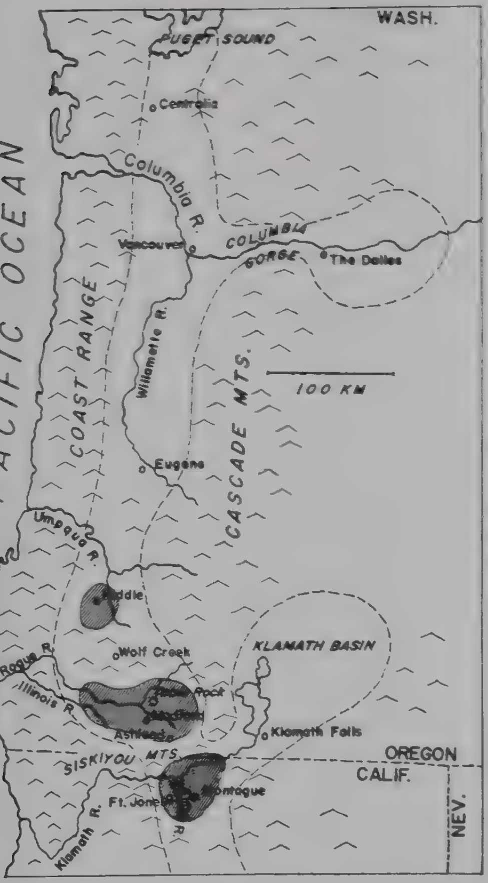

Fig. 1. Map of the study area showing present chaparral areas (cross-hatched), and probable limits of maximum postglacial extent of chaparral or its associates (broken line).

vegetation types. Moreover, for some distance north of the Rogue and Umpqua Valleys there are relict islands of vegetation containing many of the chaparral associates (Detling 1953), which are important in the study of the migrations of Pacific Northwest floral components.

Ecology of the Chaparral

Structure and Present Distribution

In southern California the chaparral is largely dominated by *Adenostoma fasciculatum. Ceanothus cuneatus* is associated with it in that area and replaces it as the dominant species in central and northern California in what Cooper (1922) terms the "climax chaparral." This *Ceanothus*-dominated chaparral occurs abundantly in the Shasta Valley, and in large areas in the Rogue River watershed in southwestern Oregon, especially at lower elevations. There it usually occupies the valley floor, which averages about 305 m in elevation, or the lower foothill slopes. However, on some of the higher ridges pure stands of chaparral may ascend to 1100 m. At middle elevations or in cooler and moister situations *Ceanothus* may either be dominant, or co-dominant with such shrubs as *Arctostaphylos* spp. It frequently occurs as the understory where deciduous oak woodland or ponderosa pine forest is clearly climax.

Patches of *Ceanothus* chaparral occur on the slopes of the South Umpqua Valley near Riddle and Myrtle Creek, but these areas are relatively small and the composition of the plant community is altered by the infiltration of non-chaparral species from the surrounding coniferous forest.

Second to *Ceanothus cuneatus* in importance among the Oregon chaparral shrubs is *Arctostaphylos viscida*. This species is less tolerant of xeric conditions than is *C. cuneatus;* it is often mixed with the latter, but at times forms pure stands. In some places where it would be expected it is replaced by *A. canescens*.

Other shrubby species which occur with greater or lesser frequency in the Rogue Valley chaparral and should be considered integral components of it are: *Cercocarpus betuloides, Eriodictyon californicum, Garrya fremontii, Rhamnus californica* var. *occidentalis, Rhus trilobata, Amelanchier pallida, and Chrysothamnus nauseosus* ssp. *albicaulis*.

The five major dominants in the vegetation of the Rogue watershed, listed in order of decreasing tolerance to xeric conditions, are *Ceanothus cuneatus, Arctostaphylos* spp., *Quercus garryana, Pinus ponderosa*, and *Pseudotsuga menziesii*.

Near Medford, which has the least precipitation and summer temperatures among the highest in the watershed, *Ceanothus cuneatus* is essentially the only chaparral component on the valley floor. *Arctostaphylos* is absent from the level plain. The oaks are also absent except for an occasional small colony where local conditions are especially favorable. Because this part of the valley has been settled for a long time it is difficult to determine to what extent oak woodland existed here, if ever, but judging from the present situation it seems probable that *C. cuneatus* is climax in this particular area.

Ceanothus ascends those slopes surrounding the valley floor where drought and temperature conditions are most extreme and where other species consequently do not compete with it. A striking example of this is seen on the south and west slopes of Upper Table Rock, which contrast with the north slope of the mesa where there is a clear, open stand of oak.

Throughout most of the Rogue Valley *Ceanothus cuneatus* is closely associated with the deciduous oaks, usually *Quercus garryana*. The oaks are more mesic in their requirements than *Ceanothus,* and form a belt just above and in contact with it on the foothill slopes. *Arctostaphylos,* especially *A. viscida,* frequently occupies a zone between the two, overlapping both. It is intermediate between them in drought tolerance. In many vigorous stands of *Ceanothus* there are oak trees in considerable numbers, usually of one size and apparently of one age. In such situations *Ceanothus* is obviously in a successional stage with the oaks probably representing the climax type. In some of these *Ceanothus-Quercus* mixtures there is evidence of fire, and according to the records of the United States Forest Service and the verbal accounts of the older inhabitants of the valley all of the brushy hillsides of the region have been periodically burned off for many years. It is probable that much of the Oregon chaparral depends upon fire for its continued existence.

Pinus ponderosa is less tolerant of xeric conditions than is *Quercus garryana,* and in the Rogue Valley it ordinarily forms a broad belt above the oaks on the hillsides. It is more closely associated with *Arctostaphylos* as a chaparral shrub than with *Ceanothus.* A large extent of the Illinois Valley floor is occupied by a mixture of *Pinus ponderosa and Arctostaphylos canescens,* the latter forming fairly dense stands. Burned pine snags and the fact that in any one local area the pines are mostly of uniform age suggest that ponderosa pine is climax here after fire, and that *Arctostaphylos* is subclimax. In the same area are patches of *Ceanothus cuneatus* in almost pure stand. This species thus overlaps *Arctostaphylos* as a chaparral plant.

None of the chaparral species is normally associated with Douglas fir (*Pseudotsuga menziesii*), which occupies the slopes above ponderosa pine and the cooler and moister canyons and draws.

The Californian chaparral area closest to that of southwestern Oregon, both geographically and floristically, is in central and northern Siskiyou County. Here the chaparral is centered in the Shasta Valley near Yreka, and extends northward into the valley of the Klamath River, principally around Hornbrook. These valleys are appreciably higher in elevation than the general level of the Rogue Valley, Yreka at 800 m and Hornbrook at 656 m. They are separated from the Rogue watershed by a ridge of the Siskiyou Mts., whose lowest point is the Siskiyou Pass with an elevation of 1362 m.

Chaparral, with *Ceanothus cuneatus* as an important member, ascends the south slopes of this ridge to about 1140 m. Above this there are extensive brush areas covered with scrub *Quercus garryana, Amelanchier pallida,* and *Chrysothamnus nauseosus* ssp. *albicaulis,* with frequent larger trees of *Quercus garryana, Juniperus occidentalis,* and *Pinus ponderosa.* There is evidence that not long ago this was a pine-oak-juniper forest which has been burned off. The north slopes of the ridge below the pass in the Rogue watershed are covered with Douglas fir forest and its usual associates.

The Siskiyou County chaparral is similar in structure to that of the Rogue watershed. *Ceanothus cuneatus* is its dominant shrub. Most of the other chaparral shrubs in the Rogue are also components of the Siskiyou chaparral. However, *Rhus trilobata,* occurring only occasionally on the Rogue, is abundant in the Klamath and Shasta Valleys, often forming large patches in pure stand. *Amelanchier pallida* is more abundant here than north of the Siskiyous. Other shrub species more in evidence in the Siskiyou County chaparral are: *Eriodictyon californicum, Lonicera interrupta, Philadelphus lewisii* var. *californicus, Prunus subcordata,* and *Rhamus crocea* spp. *ilicifolia.*

The ecological relationship of the chaparral formation to the oak woodland is apparently the same in the Shasta and Klamath Valleys as in southwestern Oregon.

Any discussion of the Rogue River chaparral calls for a comparison between it and the shrub vegetation of eastern Oregon. North of the Siskiyous the two types are separated by the Cascade Range with its conifer forests of middle and high elevations. A good picture of what the relationship would be between the two vegetation types in Oregon if they were actually in contact is afforded by the transition from the typical *Ceanothus* chaparral of the Shasta Valley to the Klamath Basin type to the east, across an area from which high elevations are absent. The transition is striking traveling eastward from Grenada, a small community 16 km southeast of Yreka. A transect from there starts from the valley floor at an elevation of 793 m and cuts across rolling hill country, but without crossing any significant topographic barriers. A gradual increase in elevation, however, probably accounts for most of the floristic change. *C. cuneatus,* common at Grenada, soon disappears, and just east of the town there are extensive areas of dominant *Chrysothamnus.* The scrub formation is gradually replaced by an open juniper woodland. At 16 km east of Grenada sagebrush (*Artemisia tridentata*) becomes an abundant associate of the juniper, and *Chrysothamnus* becomes relatively less frequent. About

8 km farther east *Arctostaphylos patula* appears, along with occasional *Purshia tridentata.* These become more abundant eastward, and at the west boundary of the Shasta National Forest, 32 km east of Grenada at about 1220 m, *Purshia, Artemisia,* and *Arctostaphylos patula* are the dominant shrubs. There also juniper is being replaced by ponderosa pine. These species continue northward and eastward into the Klamath Basin, dominating the vegetation in that area. At some places on the slopes bordering the eastern edge of the Shasta Valley the brush associated with *Pinus ponderosa* consists of *Ceanothus cordulatus* and *Prunus emarginata,* either of which may occur in abundance. These two species, with *Arctostaphylos patula* and *Ceanothus velutinus,* make up an important part of what Cooper calls the "conifer forest chaparral." With the exception of *Ceanothus cordulatus* they range northward east of the Cascades as associates of the ponderosa pine forest, especially in its cooler and moister phases, being replaced in its drier phases by *Purshia.* The association does not occur typically west of the Cascades in Oregon or Washington.

Climatic Requirements

There are 5 widely separated regions where chaparral, under various names, occurs as a distinct plant formation: (1) the Mediterranean region, (2) the coast of southwestern Africa, (3) southern and southwestern Australia, (4) central Chile, and (5) California. The major climatic features of these regions are similar: a relatively low total precipitation with a period of summer drought, and no more than a moderate difference between seasonal temperature extremes. Cooper (1922) found that in California the broad-sclerophyll vegetation, which includes the chaparral, is the dominant type in those areas having a mean total annual rainfall from 250-760 mm, where the summer rainfall is less than 20% of the annual total. The temperature extremes in the coldest and hottest months are moderate; the minima are decidedly higher in the chaparral belt than in other formations.

Table I, compiled from the official records of the United States Weather Bureau (U. S. Dept. Agric. 1941, U. S. Dept. Comm., n.d.), presents pertinent precipitation and temperature data for (1) selected stations in the chaparral areas of southwestern Oregon and central Siskiyou County, California, and (2) additional stations outside the present chaparral formation in areas which are of interest for comparative and historical purposes.

In compiling the data for this table, summer precipitation for each station was calculated by adding the means of the 6 driest months. This drought period in all cases coincides with the period of highest temperatures. Temperature extremes during both winter and summer are probably more significant to plant distribution than average temperatures during those periods. This is the reason for incorporating into the table the columns for January mean minima and July mean maxima rather than the daily means for those months.

TABLE I. Climatic data

Station	PRECIPITATION (mm)			TEMPERATURE (°C)	
	Total Annual	Total Summer	% Summer	January Mean Min.	July Mean Max.
Montague	312	84	27	−4.3	33.7
Ft. Jones	533	106	20	−5.8	33.1
Medford	419	109	26	−2.7	31.7
Modoc Orchard	516	105	20	−2.2	32.8
Grants Pass	742	128	17	−0.4	32.2
Riddle	725	152	21	0.7	30.5
Ashland	502	140	28	−1.5	29.9
Siskiyou Summit	825	180	22	−3.7	24.2
Wolf Creek	972	155	16	−0.4	30.8
Mt. Shasta	870	146	17	−4.2	29.1
Klamath Falls	314	83	26	−6.2	29.4
The Dalles	347	67	19	−2.6	31.1
Eugene	962	233	24	0.8	27.8
Vancouver	944	233	25	0.3	26.7
Centralia	1159	276	24	0.2	26.4

The 7 stations of the first group in Table I are representative of the chaparral belt. Of these, Ashland is at the upper limit of the formation, on the lower north slope of the Siskiyou Mts. Montague is approximately at the center of the Shasta Valley, in northern California, which is covered by extensive areas of chaparral similar to that in Oregon. Ft. Jones, in the Scott River Valley, is in the same general chaparral area. Medford, Modoc Orchard (on Upper Table Rock near Medford), and Grants Pass are representative of the main valley of the Rogue River. Riddle is near the center of such patches of chaparral as occur in the South Umpqua Valley; this station is about at the present northern limit of the chaparral. The next two stations are associated with the physiographic features which separate the 3 river basins in which chaparral occurs; Siskiyou Summit on the high ridge separating the Klamath River Valley from the Rogue, and Wolf Creek in the less elevated cross range between the Rogue and Umpqua watersheds. The remaining stations, outside the chaparral areas, will be discussed later.

In the first 7 stations the precipitation figures are mostly well within or close to the limits found by Cooper (1922) for the California chaparral. The obvious exceptions are the high summer percentages at Ashland, Medford, and Montague;

Ashland, however, is at the upper limit of chaparral, and the dominance of chaparral at Medford and Montague, in spite of the relatively high summer rainfall is doubtless due to the low absolute amount of summer and annual precipitation.

The role of the Siskiyou Mts. in isolating the present Rogue Valley chaparral from that of the Klamath and Shasta Valleys of northern California is explained by the climatic data for Ashland and Siskiyou Summit in Table I. Ashland's mean annual precipitation is well within the limits optimum for chaparral, but its total summer precipitation is higher than that of more typical chaparral stations, both in actual amount and relative to the annual total. This feature, combined with a slightly lower July temperature which would affect the evaporation rate during the drought period, probably eliminates the chaparral at this point. Between Ashland and the summit there is a significant increase in both annual and summer rainfall, although the summer percentage decreases. In temperature, both summer maxima and winter minima are lower at the summit. The entire north slope of the ridge above Ashland is covered by conifer forest.

Unfortunately there are no available climatic data showing the rainfall and temperature gradients on the south slope of the ridge. At first it might seem that the low winter minimum temperatures on the ridge (—3.7°C at Siskiyou Summit) might be the important factor limiting the spread of chaparral upward from the Klamath River Valley, especially since *Chrysothamnus* and *Amelanchier,* the only shrubby members of the chaparral which do ascend the south slopes of the ridge as far as the summit, are adapted to cold winters east of the Cascade-Sierra axis. However, it is more likely the combination of a relatively high summer precipitation with a low maximum summer temperature that fosters the juniper-scrub oak growth prevalent on the south slopes below the summit.

Transverse ridges between the Cascades and the Oregon Coast Range are effective barriers today to the further northward spread of the Rogue River chaparral, and isolate the chaparral area of the South Umpqua Valley. These cross ranges are occupied by a conifer forest, from which even small patches of oak woodland are mostly absent. The reason for this is suggested by the high annual rainfall, of which the mean of 972 mm at Wolf Creek is representative.

North of the chaparral areas, ie., in most of the Umpqua Valley, all of the Willamette Valley, and the valleys of western Washington, the region has summer drought, mild winters and moderately cool summers, but the high annual precipitation permits a conifer forest to dominate except for local patches of oak woodland.

The mid-Columbia region, of which the climatic data for The Dalles are taken as representative, is comparable with most of the typical chaparral stations in its low annual precipitation and in both summer and winter temperature means. The only factor which is extreme is the summer drought. This might be the limiting one at present in this area, or possibly chaparral was excluded from the area by other conditions earlier in its history, and more recently has not been able to cross the barrier imposed by the Cascade Range.

The climatic means for the lower elevations of the Klamath Basin are in general not greatly different from those of the mid-Columbia area, as may be seen by comparing the data for Klamath Falls with those for The Dalles. However, Klamath Falls does have a January mean minimum much lower than that of The Dalles. This suggests that colder winters either prevented the spread of chaparral as a formation into areas east of the Cascades in the first place, or eliminated it more recently.

FORMER RANGE OF THE FORMATION

Fossil Record

During the last 2 or 3 decades studies of fossil floras of western North America have shed light on the origin of chaparral as a type on this continent. The results of this research have been summarized and interpreted by Axelrod (1958). The evidence indicates that sclerophyll vegetation, including chaparral, was derived during the early and middle Tertiary from tropical and temperate floras that made up the Madro-Tertiary Geoflora in northern Mexico and southwestern United States. This vegetation spread into the Great Basin and California as a result of a progressive drying of the climate of the western part of the continent, and reached its greatest northward extension during the Middle Pliocene. With the continuing elevation of the Cascade-Sierra axis during this epoch the Great Basin climate became more continental, and probably due to colder winters the chaparral and most other sclerophyllous types were eliminated by the Late Pliocene. Related species, however, have persisted in California and Baja California and make up the chaparral found there today. The more recent history of the Northwestern chaparral is involved in postglacial climatic fluctuations.

Relict Occurrences

Although a chaparral formation does not now occur farther north than the central part of the Umpqua watershed nor east of the Cascade-Sierra axis, there is reason to believe that it was once more widespread, at least west of the Cascades. Within the forested areas, but in restricted situations where neither conifers nor oaks have been able to establish themselves, such as rocky outcrops on steep slopes or ridge crests, are frequently found relict islands of xeric herbaceous vegetation which today is typical of the Rogue Valley (Detling 1953). The deep-rooted chaparral shrubs, because of this shallow soil, may never have established themselves in these situations. Judging from occasional small patches of *Ceanothus cuneatus* on well-drained soils in the Willamette Valley, such as those overlying old gravel bars, it seems probable that chaparral occupied this northern area during a period when rainfall was much less than at present. With a later increase in general precipitation the oak woodland and conifer forest must have crowded the chaparral and its associates out of the deeper soils of the valleys, but did not succeed in displacing the associates from the more shallow-soiled islands. *Garrya fremontii* occurs as far north as the upper Willamette Valley, and *Chrysothamnus nauseosus* spp. *albicaulis* sporadically in xeric islands as far north as Iron Mt. on the South Fork of the Santiam River. With the exception of these 3 species none of the shrubby members of the Oregon chaparral has been reported beyond the Umpqua River, and most of them go no farther than the Rogue.

Distribution of Chaparral Associates

A number of the herbaceous species which in the Rogue Valley are typical associates of the chaparral have interesting and significant distributions. In noting the occurrence in northwestern Oregon of islands of xeric vegetation of southern affinities (Detling 1953), I did not attempt to distinguish the typical chaparral species from those of other associations. However, closer investigation shows that many of the xeric relicts of the north are chaparral associates in the Rogue Valley and northern California. An examination of the present distribution of the chaparral associates should throw some light on the recent history of the formation in the Pacific Northwest.

I have not attempted to compile a complete flora of the chaparral region under consideration. The 183 species from which the plant lists in the following pages are drawn were collected during numerous field trips in southwestern Oregon and northern California from 1940 to 1957, and more intensive study of the chaparral during the spring and summer of 1958 and 1959. These are the species which I found associated with *Ceanothus cuneatus;* they and others, however, also occur in other chaparral types, such as that dominated by *Arctostaphylos.* I felt that limiting the working list to species definitely associated with the most characteristic shrub of the southwestern Oregon chaparral would give a well defined and reliable basis for this study.

I have found that the species distributions fall into a small number of definite patterns. In defining and briefly discussing each in the following paragraphs I have indicated the number of species, and the percentage of the total of 183, which follow each pattern, and have cited representative examples from each group without attempting to list all the species. Authorities for the specific names used will be found in the regional manuals by Peck (1941), and Munz (1959).

Following are the 7 "patterns" which I have recognized. Within the geographical limits stated, all the species when occurring beyond the chaparral belt grow typically at low elevations in the valleys and in warm, dry canyons. They frequently occur in oak woodland and sometimes in ponderosa pine forest.

Pattern I.—(44 species—24%). From California northward into the Rogue area, including the central part of the Umpqua Valley. Species of this group may have relict outposts farther north, but they do not occur east of the Cascade Mts.

Representative species: *Arctostaphylos canescens, A. viscida, Arenaria californica, Astragalus pacificus, Baeria chrysostoma* ssp. *gracilis, Ceanothus cuneatus, Chlorogalum pomeridianum, Eriodictyon californicum, Frasera albicaulis* spp. *nitida, Fritillaria recurva, Lonicera interrupta, Monardella villosa* var. *subserrata, Rhamnus californica* spp. *occidentalis, Sidalcea malvaeflora* ssp. *asprella, Thysanocarpus radians, Trifolium depauperatum.*

Pattern II.—(19 species—10.4%). From California north to the Puget Sound region, including southern British Columbia, west of the Cascade-Sierra axis. The species are closely allied ecologically to those of Pattern I. They become less abundant as they go northward from the Rogue Valley, and the line of demarcation between these and the typical Pattern I species with occasional relict occurrences to the north is not too well defined.

Representative species: *Calochortus tolmiei, Garrya fremontii, Madia madioides, Rhus diversiloba, Silene campanulata* spp. *glandulosa, Trichostemma lanceolatum, Trifolium albopurpureum.*

Pattern III.—(17 species—9.3%). From California through the Rogue area where they are usually very abundant; northward in varying degrees of abundance to Puget Sound, and along the Columbia River and its tributaries in north central Oregon and south central Washington. They may usually be found in the Columbia River

Gorge, particularly on the south slopes of the Washington side. Some of the species which are common in the Rogue area and in the mid-Columbia region occur as rare xeric island plants elsewhere west of the Cascades; in a few instances there is no record of even these intervening occurrences.

Representative species: *Linanthus bolanderi, Lupinus bicolor, L. micranthus, Navarretia tagetina, Orthocarpus attenuatus, Pectocarya pusilla, Plagiobothrys nothofulvus, Quercus garryana, Tonella tenella.*

Pattern IV.—(6 species—3.3%). California north to Puget Sound, most abundant in the Rogue Valley or southward; east of the Cascades in the mid-Columbia area at the head of the Columbia Gorge, and in the Klamath Basin. Apparently there are no known occurrences of any of these species east of the Cascades between the mid-Columbia area and the Klamath Basin. The northern arm is connected with the main body of the population through the Columbia Gorge, while the Klamath Basin plants have a direct connection to the south with the population of the Shasta Valley. This is a small group whose members are least abundant (often rare) in the Klamath Basin.

Representative species: *Agoseris heterophylla* var. *normalis, Balsamorhiza deltoidea, Brodiaea coronaria, B. pulchella.*

Pattern V.—(17 species—9.3%). California, west of the Sierra Nevada, to the valleys of the Siskiyou Mts.; thence extending northward in two arms, one into the Rogue area, the other into the Klamath Basin.

Representative species: *Asclepias cordifolia, Castilleja pruinosa, Cercocarpus betuloides, Convolvulus polymorphus, Cornus glabrata, Lomatium californicum, Mahonia piperiana, Micropus californicus, Prunus subcordata.*

Pattern VI.—(22 species—12%). A basic distribution through California west of the Sierra Nevada to the Siskiyou Mts. or Modoc County, then north and east for varying distances east of the Cascades, but always beyond the Klamath Basin. A few species, besides having this basic distribution, extend into the Rogue Valley where they may occur abundantly.

Representative species: *Amelanchier pallida, Chrysothamnus nauseosus* ssp. *albicaulis, Cryptantha torreyana, Penstemon laetus* spp. *roezlii, Rhus trilobata, Stylocline filaginea.*

Pattern VII.—(58 species—31.6%). Of relatively wide distribution in the Pacific States. Both sides of the Cascade-Sierra axis, usually from southern California to Canada and frequently east to the Rocky Mts. Typically species of dry, open situations, but because of their wide distribution and common occurrence in other vegetation types they are not significant in an interpretation of the chaparral, where they apparently occur only incidentally.

Representative species: *Amsinckia intermedia, Brodiaea hyacinthina, Chaenactis douglasii, Clarkia rhomboidea, Madia exigua, Myosurus minimus, Penstemon deustus, Plagiobothrys tenellus, Prunus emarginata, Scutellaria antirrhinoides, Thysanocarpus curvipes.*

Discussion

Californian Origin of the Chaparral

Historically the southwestern Oregon chaparral is obviously bound to that of California. There is a close floristic relation between the two areas. Many species are common to both; in other cases species in the one area are represented in the other by closely related species or subspecies. On the other hand, not only has chaparral as a vegetation type long been eliminated from the northern Great Basin, but relatively few typical Rogue River chaparral associates range east of the Cascade-Sierra axis into the Great Basin; this minimizes the likelihood that the Rogue chaparral ever migrated to its present area from east of the mountains. No occurrences of the chief chaparral species, *Ceanothus cuneatus*, are known east of the Cascades. A few of the other shrubby members of the formation, namely *Cercocarpus betuloides, Mahonia piperiana, Prunus subcordata,* and *Amelanchier pallida,* occur more or less sporadically in the Klamath Basin today.

Postulated Climatic Changes

Since the Rogue Valley is the northernmost outpost of typical North American chaparral today, it may be assumed that the climate of the whole northwest region occupied by chaparral at its greatest extent had the general features of the present Rogue climate. This is characterized by low annual and summer rainfall, mild winter temperatures, and moderately high summer temperatures, as compared with adjacent vegetation areas. An "intensification" of these factors, i.e., a decrease in rainfall and an increase in either summer or winter temperatures, would tend to extend the type of vegetation most dependent upon such extremes, namely chaparral. From the data in Table I we can postulate the climatic changes necessary to bring about the spread of chaparral over the present topographic-ecologic barriers and into the areas it probably once occupied in the Pacific Northwest. Since the Rogue Valley chaparral undoubtedly came from the south, but is now isolated from its California relatives by an effective barrier, the Siskiyou Mts., it will be significant to include climatic changes that would permit the formation to cross this barrier in the first place, rather than to assume a population already present north of the Siskiyous from which a migration could start.

In view of the January mean minimum temperatures of —4.3°C and —5.8°C at Montague and Ft. Jones respectively, in the heart of some of the most extensive and most typical *Ceanothus* chaparral, it seeems unlikely that the winter temperatures at the altitude of the Siskiyou Pass (—3.7°C) are severe enough to prevent the upward movement of chaparral on the south slopes to the low points of the ridges and thence into the Rogue watershed. The critical point in winter minima for chaparral is probably between the —5.8°C of Ft. Jones and the —6.2°C of Klamath Falls. A general increase in winter temperatures sufficient to raise the January mean minimum by 1°C only would bring the Siskiyou Summit mean up to the present mean at Medford and make it comparable with those of other typical Rogue River chaparral stations. Such an increase would raise the Klamath Falls mean minimum to —5.2°C, which should allow the development of chaparral in the Klamath Basin if other factors were favorable. The present winter minima at The Dalles are within the range of those in the Rogue chaparral.

July maximum temperatures are noticeably higher in the chaparral belt than at the pass on the Siskiyou Mts. barrier. The latter is more comparable in summer temperatures with the valleys that extend northward west of the Cascades to Puget Sound. There is little difference between the July mean maximum at Klamath Falls and those of Ashland, Mt. Shasta, and Wolf Creek, all of which either coincide with or are just above the upper limit of chaparral. The Dalles also is close to the typical Rogue chaparral stations in July maxima.

The average July maximum for the 7 chaparral stations of Table I is 32.0°C; the average for Eugene, Vancouver, and Centralia is 27.0°C. There is thus a difference of 5.0°C between the typical chaparral area and the more northern area where only chaparral relicts occur. A general increase throughout the Pacific Northwest of 5.0°C in summer maximum temperatures would bring the Siskiyou mean to 29.2°C, just within the limits required for chaparral; it would raise the Klamath Basin mean to 34.4°C, that of the Dalles to 36.1°C, the general mean throughout the Williamette Valley and southwestern Washington to 32.0°C, and in the Rogue and Shasta Valleys to about 37.0°C. These high summer temperatures at The Dalles and in the Rogue Valley are probably well above the optimum for the development of chaparral. In California Cooper (1922) found such summer temperatures only in the desert and in the grasslands of the Central Valley.

Precipitation was probably as important a factor as temperature in the northward migration of chaparral. The present average annual rainfall of the 7 chaparral stations ranges from 312 mm at Montague to 742 mm at Grants Pass. A reduction of only 83 mm would be required to make Siskiyou Summit comparable in this respect with Grants Pass. On the same basis, however, it would require a decrease of about 230 mm in the annual rainfall at Wolf Creek to bring this figure to where chaparral could successfully compete with the conifer forest and cross the low mountain barrier into the Umpqua and Willamette Valleys and southwestern Washington. Rainfall at Wolf Creek is fairly typical of the present climate of these more northern valleys, at least as far as Centralia, and it appears reasonable that at the time of maximum northern advance of the chaparral this region had at least 230 mm less annual rainfall than at present.

Such a reduction in precipitation from the present means at Montague, Medford, Klamath Falls, and The Dalles would have resulted in amounts below the 250 mm found by Cooper (1922) to be the lower limit for chaparral. The combination of this extreme drought condition and the hot summers suggests the likelihood of restricted areas in the Rogue Valley and in the lowlands about The Dalles of some formation other than chaparral, probably grassland. In the mid-Columbia area drought conditions above the Columbia Gorge could have prevented the invasion of chaparral from the Gorge and may explain the absence today of any trace in this area of the Rogue xerophyllous scrub.

In the Klamath Basin the situation in regard to general precipitation is similar to that in the mid-Columbia. However, the fact that several shrubby chaparral species came into the Klamath Basin and still persist there points to the probability that during the xerothermic maximum summer temperatures in this region were not severe enough to cause Great Basin types, such as sagebrush, to replace or completely exclude the chaparral types.

Postglacial Migrations of Chaparral

The foregoing discussion suggests the probable postglacial history of the chaparral in Oregon and Washington. We may assume the presence in California of a chaparral association similar in floristic structure and ecologic requirements to that now in the Shasta Valley. A major climatic change probably decreased annual precipitation to about 230 mm below present means and increased winter minimum temperatures by at least 1.0°C and summer maxima by 5.0°C. This hypothesis is substantiated by the work of Hansen (1955). In pollen analyses of Northwestern bogs he demonstrated the beginning of a warming and drying trend about 8000 yrs ago which persisted for 4000 yrs, gradually giving way to a cooler and moister climate. The changes apparently resulted in the following phenomena:

a) The California chaparral moved northward, crossing the ridges of the Siskiyou Mts. at their lowest points in southern Josephine County, Oregon. Ecologic barriers in other cross ranges having been eliminated by the climatic change, it migrated northward between the Cascade and Coast Ranges as far as the valleys of southwestern Washington. At the time of greatest northward extension of the chaparral drought and summer temperature extremes in the Rogue watershed were probably such that chaparral was replaced by grassland on the floor of the main valley but continued to occupy the surrounding foothills and lower mountain slopes. This situation may have existed also in parts of the Umpqua and Willamette Valleys, and may have been the origin of the grasslands that persisted there to the advent of white man.

b) Chaparral migrated by way of the Shasta Valley northeastward into the Klamath Basin; there was no significant physiographic and ecologic barrier to this movement. It apparently did not extend beyond the Basin.

c) By the time the chaparral extended as far north as the Columbia River west of the Cascades drought and hot summers in the mid-Columbia area probably were not conducive to the migration through the Columbia Gorge of the shrubby species comprising the formation, although at some period, under less xeric conditions, the Garry oak woodland invaded the area from the west. An extensive region above the Gorge probably developed a grassland, perhaps bordering on desert conditions, and into this, by way of the Gorge, migrated many of the herbaceous chaparral associates.

d) With the return of moister and cooler conditions west of the Cascades, oak woodland and conifer forest have become more generally dominant, occupying the cross ranges again and restricting the chaparral to isolated basins in the south and occasional relicts northward. In the Rogue Valley chaparral has moved downward from the foothill slopes and competes successfully in most places with the grassland of the valley floor.

e) Severe winters east of the Cascades have eliminated chaparral as a formation from the Klamath Basin, although a few of its shrubby members persist there as occasional associates of other formations. In the mid-Columbia area above the Columbia Gorge, a rather large number of herbaceous chaparral associates, mostly annuals and bulbous perennials, have persisted either in the oak woodland or on open grassy slopes.

SUMMARY

The chaparral formation of the Pacific Northwest is confined to the Rogue River watershed and a few small areas in the South Umpqua Valley, Oregon. Floristically it is related to the chaparral of central and northern California, with *Ceanothus cuneatus* and *Arctostaphylos* spp. as its chief shrub constituents.

The most significant climatic features of the chaparral belt of the Rogue and Shasta Valleys are: (1) mean annual precipitation between 312 and 742 mm, (2) summer precipitation from 17% to 28% of the annual total, (3) mean winter minimum temperatures from —5.8° to 0.7°C, and (4) mean summer maximum temperatures from 29.9° to 33.7°C.

In southwestern Oregon chaparral is the most xeric in requirements of all the vegetation types, and in most situations is subclimax to oak woodland or ponderosa pine forest.

Relict occurrences of *Ceanothus cuneatus* and the distribution patterns of the Rogue River chaparral associates indicate that chaparral once extended northward almost to Puget Sound. Judging from known climatic requirements of the present California and Oregon chaparral, a decrease of about 230 mm in annual rainfall below the present means, accompanied by a rise of at least 1.0°C in winter minimum and 5.0°C in summer maximum temperatures must have occurred to cause such an extension of the formation. During such a xerothermic phase chaparral also occupied the Klamath Basin east of the Cascade Mts. Many of its associated species migrated through the Columbia Gorge and mingled with what was probably a grassland formation in the mid-Columbia region.

REFERENCES

Axelrod, D. I. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. **24**: 433-509.

Cooper, W. S. 1922. The Broad-sclerophyll vegetation of California. Carnegie Inst. Wash., Publ. **319**. 1-124

Detling, L. E. 1953. Relict islands of xeric flora west of the Cascade Mountains in Oregon. Madroño **12**: 39-47.

Hansen, H. P. 1955. Postglacial forests in south-central and central British Columbia. Am. Jour. Sci. **253**: 640-658.

Munz, P. A. 1959. A California flora. Univ. of California Press, Berkeley and Los Angeles.

Peck, M. E. 1941. A Manual of the higher plants of Oregon. Binfords and Mort, Portland.

U. S. Dept. of Agriculture. 1941. Climate and Man. Yearbook of Agriculture, 1941. Govt. Printing Office, Washington.

U. S. Dept. of Commerce (Weather Bureau). No date. Climatic summary of the United States—supplement for 1931 through 1952. California, Oregon, Washington.

THE SPRUCE-FIR FORESTS OF THE KEWEENAW PENINSULA, NORTHERN MICHIGAN

Paul F. Maycock
Department of Botany, McGill University, Montreal, P. Q.

Introduction

The forests of the northern peninsula of Michigan form a segment of an extensive forest system that stretches throughout the northern Great Lakes region. Although these forests possess unique structural and compositional features, they are best understood by recognizing that many of these characteristics are a consequence of a gradual vegetational transition from pure deciduous forest communities farther south, through deciduous-conifer mixtures to pure coniferous types in more northern regions (Nichols 1935, Maycock and Curtis 1960). Within this transition slight modification of existing local environmental conditions might favor one of these forest communities to the disadvantage of the others. Similarly, established forests may embody characteristics of the several communities.

Within this region, the Keweenaw peninsula (Lat. 47° N., Long. 88°90′ W.) extends into Lake Superior almost 45 miles from its southern shore. The more northern geographical position of the peninsula coupled with the climatic influences of the lake provide a situation where environmental influences are more delicately balanced than in adjacent areas. These conditions are reflected in the great variety of forest vegetation throughout the peninsula and particularly in the occurrence of distinctive boreal forest communities toward the northern extremities.

In the summer of 1955 the Keweenaw peninsula (Fig. 1) was visited during an extensive survey of boreal conifer and boreal conifer-deciduous forests throughout the Great Lakes region (Maycock and Curtis 1960). Several fine examples of these communities were located in the northern sections of the peninsula. The composition and ecological status of these forest communities is considered important since they form a unit in themselves, largely because of their isolation and southern position. The ecological relationships of spruce-fir vegetation in this area are fairly typical of those found elsewhere in the region. This quantitative analysis of representative stands provides useful information on the composition and phytosociological relationships and is presented to assist in providing a quantitative basis for the enumeration of boreal forest communities which have been only generally described for this region. This report should also extend the understanding of the entire spruce-fir formation in North America.

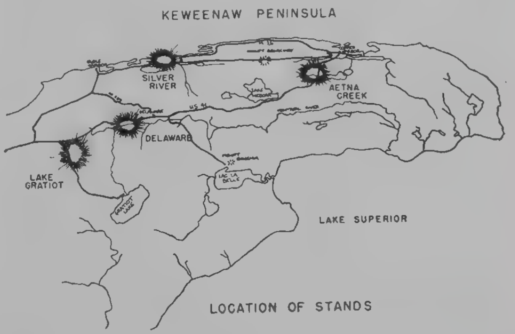

Fig. 1. Map of the northern section of the Keweenaw peninsula (Keweenaw county, Northern Michigan) showing the distributions of stands studied.

The Keweenaw has been an interesting locality for botanical research. It has long been a center of human activity concerned especially in the mining of copper and has been of considerable historical importance in the settlement of the Lake region.

This study was supported by the generous assistance of the Wisconsin Alumni Research Foundation. The writer wishes to express appreciation for the assistance of Dr. John T. Curtis, Botany Department, University of Wisconsin.

DESCRIPTION OF THE REGION

Environment

The floras and vegetation of peninsulas and islands present a fascinating appeal to the botanist. This is partly due to the terminable nature of such studies but also to the possibility of more sharply limiting ecological conditions which result from position. Remarkably similar forest vegetation of the type found on the Keweenaw peninsula exists on other extensive peninsular areas of the northern Great Lakes region, particularly the Bruce peninsula of Lake Huron in Ontario (Klugh 1912) and the Door peninsula of Wisconsin in Lake Michigan (Fuller 1950). These peninsulas support interesting floras and many elements considered to be representative of cordilleran populations are purported to occur there.

Publications on the floristic aspects of the Keweenaw include a discussion of supposed cordilleran disjuncts (Fernald 1935) and reports on the moss (Steere 1937, 1938) and lichen floras (Thomson 1951). The vegetation of the area has been briefly described (Braun 1950) but quantitative studies of plant communities are not available.

The past history of the area is an important consideration in regard to human activities and the way they have affected vegetational development. The reserves of native copper on Isle Royale, 50 miles northwest, resulted in extremely heavy use of the peninsula by the Copper Culture tribes (Van Pelt 1949). The northern tip served as a stepping stone to Isle Royale and hunting and camping activities in this area undoubtedly influenced the vegetation. Today, however, few experienced persons would attempt a crossing in an open boat with a powerful motor whereas the Indians crossed to the island in birch bark canoes.

Missionaries and explorers visited this area around 1675 and settlement occurred subsequently. Copper Harbor, at the northern extremity served as a refuge during storms and early wood-burning ships often refueled there. Thus logging operations of the past were probably as great a drain on the forest resources as those of the present day. Mining activities and many other kinds of disturbance including fire, wind and perhaps spruce budworm outbreaks have undoubtedly influenced the development and composition of present day vegetation.

Topographical features and geology are other factors important in permitting the development of a variety of forest communities. The area is underlain by Precambrian rocks. The peninsula originated from a ridge of resistant rocks which rise from 735 ft above Lake Superior to 1337 ft at Brockway Mountain, the highest point. This main ridge is flanked by scattered morainal deposits. The effect of glaciation in an area of such rugged topography has undoubtedly been a major factor in producing a variety of environmental situations characterized by extremes. Microclimatic situations are also provided by the many deeply cut streams which break up the northern shoreline (Van Hise and Leith 1911).

Climatic data are available for Eagle Harbor at the northern extremity of the peninsula (U.S.D.A. 1941). The surrounding waters of Lake Superior appear to have a moderating effect on prevailing climate. Narrow belts extending along the shores of Lake Michigan and Lake Superior have a modified marine type of climate and most of the Keweenaw is so affected. The average temperature for January is 16.8°F and for July is 61.7°F. Maximum temperature recorded is 100°F and a minimum of —26°F has occurred. The annual precipitation is 29 in. The peculiar geographic position in Lake Superior has produced a distinctive set of climatic conditions. Parts of the peninsula may receive 115-130 in. of snow, one of the highest snowfalls in Eastern North America. Excessive snowfall and other critical climatic influences, especially length of the growing season (147 days), may help to explain the appearance of isolated spruce-fir communities.

Vegetation

In southern sections of the peninsula deciduous forest dominated by *Acer saccharum, Betula lutea* and *Tilia americana* forms the predominant vegetation. This forest community persists wherever soils are of considerable depth and mesic conditions of moisture prevail. Toward the extreme northern sections forests composed almost entirely of boreal coniferous species (*Abies balsamea, Picea glauca*) are encountered wherever environmental conditions permit them to compete favorably with the more aggressive deciduous tree species. Throughout the peninsula, forests composed of mixtures of the dominants of these two main forest communities, often with *Pinus strobus* included with the other conifers, also occur. In low-lying wet areas *Larix laricina, Thuja occidentalis, Abies balsamea* and *Picea mariana* are the prevalent forest makers. The vegetation may thus be described as a mosaic of the forest communities of the northern Great Lakes region, with individual species occurring wherever environmental conditions are best suited to it.

These forests have been included in many broad vegetational classifications. Weaver and Clements (1938) included the area in their "Lake Forest" region. *Pinus strobus* may be locally abundant but the other important conifers (*P. resinosa* and *Tsuga canadensis*) which were considered important dominants of this region are not often found in the northern Keweenaw. Shantz and Zon (1924), in mapping the vegetation, showed the upper quarter forested by spruce-fir. Cunningham and White (1941) indicate a preponderance of hardwood forest in the interior and present a patchy localized distribution for spruce-fir. Braun (1950) includes the Keweenaw peninsula in the Superior Upland Section of the Hemlock-White Pine-Northern Hardwoods Region of the Deciduous Forest. Her descriptions support the mosaic vegetation of northern hardwoods and spruce-fir, already described. These different approaches of workers who have attempted to pigeon-hole the vegetation of this area as well as that of the northern Great Lakes region are often quite contradictory. This should illustrate the futility of trying to fit non-homogeneous vegetation into precise classification systems which have relatively little meaning. It should also emphasize the importance of a quantitative approach.

METHODS

The stands studied were sampled during the third week in August, 1955. Only stands on upland drained sites, of at least 10 acres in extent and free from unnatural disturbance during the lifetime of the existing stand, were selected for survey. An additional prerequisite concerned the homogeneous characteristics of the dominant tree layer. The stand was observed generally for homogeneity before sampling and subsequently the 4 quarter segments of tree data for major tree species were required to be similar to the extent of 20%, as determined by a chi square test. The locations of the 4 stands are mapped in Figure 1.

The Aetna Creek Stand (s.w. 1/4 sec. 6 T. 58 N. R. 28 W., Keweenaw County) is 2 miles south of Copper Harbor on U. S. Route 41. It occupies approximately 15 acres and representatives of the tree layer had attained ages of from 75-85 yrs. The presence of charcoal indicated a previous fire that may not have entirely destroyed the tree canopy and may have been limited to the ground cover. The presence of a high water table and luxuriant ground vegetation indicated a wet-mesic moisture regime.

The Silver River Stand (s 1/2 sec. 34 T. 59 N. R. 30 W., Keweenaw County) occurs approximately 2 miles southwest of the point where the Silver River crosses Michigan Hy. 26. The age of this tract is 40-50 yrs and it is apparently a young forest. Abundant *Populus tremuloides* and *Betula papyrifera* mixed with *Abies balsamea*, and comparatively little *Picea glauca*, give the impression of an intermediate successional stage. The *Populus* and *Betula* were becoming decadent and overtopped by *Abies* and this supported this impression. In certain locations the tree canopy was somewhat sparse and a heavy undercover had developed. Shallow soils with sporadic outcrops, location on a steep north-facing slope, and observations of general moisture conditions, all indicated a dry-mesic site. The approximate size of the stand is 25 acres.

The Delaware Stand (s.e. 1/4 sec. 17 T. 58 N. R. 30 W., Keweenaw County) is located 1½ miles west of Delaware on U. S. Route 41. Topography was described as very gently rolling to level and moisture conditions as mesic. This forest is typically spruce-fir although a scattering of *Pinus strobus* and *Populus tremuloides* is found throughout. *Picea glauca* and *Abies balsamea* originally seeded in thickly but as the stand has aged severe competition has resulted in considerable natural thinning. Wind has affected this thinning process by removing the unhealthy and dying specimens and occasionally a living member from the canopy. The age of the stand exceeded 100 yrs and it was approximately 20 acres in extent. There were indications of previous fire.

The Lake Gratiot stand (w. 1/2 sec. 25 T. 58 N. R. 31 W., Keweenaw County) is boreal conifer-hardwoods and dominated by *Acer saccharum* and *Abies balsamea*. *Picea glauca* and *Pinus strobus* are other important tree species. It is situated one mile south of U. S. Route 41 on the Gratiot Lake Road. The moisture conditions were mesic. The size of the stand is approximately 45 acres and topography is continuously moderate, varying from very gently rolling to level. In a few stations there was local evidence of windthrow, affecting particularly the coniferous species. The stand was at least 130 yrs old.

Additional stands of spruce-fir or spruce-fir-mixed hardwoods were observed during a reconnaissance of the peninsula. Mature stands occur near Mount Bohemia; on the northeast shore of Laket Gratiot; near Mud Lake on County road 586; south of Vaughnsville on Michigan Hy. 26; on the south shore near the mouth of Winters Creek; and near Gay. This vegetational community is thus well established in the area. The stands selected for intensive analysis represented the variety of spruce-fir communities which are found growing over a broad range of moisture conditions.

In sampling the tree canopy and the sapling layer the Quarter method as discussed by Cottam and Curtis (1956) was employed. Sampling points were spaced at 25 yd intervals along lines which passed well within stand boundaries and avoided marked changes in topography and moisture conditions. Line directions were selected at random. Forty points were sampled in each stand, except in the Delaware tract in which 30 were taken. Square metre quadrats to record the frequencies of all tree seedlings, shrubs and herbs were laid at every other point. The presence of all trees, shrubs and herbs in the stand was recorded during an initial inspection and during the sampling process. Those woody stems 12 sq in. or greater in basal area at breast height were considered trees. Saplings were woody stems between one in. diameter and 12 sq in. basal area at breast height. Smaller woody stems were considered tree seedlings. Nomenclature is referred to Fernald (1950).

RESULTS

Field data indicating the composition of tree, shrub, and herb layers were summarized to present overall composition and to permit a comparison of individual stands. Frequency, density and dominance values were calculated for each tree species in each stand. Each of these individual values was converted to a relative value on the basis of the entire data for each measure in the total tree complement of each stand. Subsequently, relative frequency, relative density and relative dominance were summed to establish an importance value for each tree species in each stand. Importance values for all tree species in each stand sum to 300 (Curtis and McIntosh 1951). Frequency values were determined for each shrub and herb species as per cent occurrence in all quadrats in each stand.

A total of 18 species was included in the quantitative data for tree composition. Of this number, *Acer spicatum, Amelanchier sp.* and *Alnus rugosa* rarely attained the tree canopy but were usually confined to the sapling layer or a stratum intermediate between the sapling and tree layer. Of the other trees, *Pyrus americana, Ulmus americana, Acer rubrum, Betula lutea, Quercus rubra, Larix laricina, Tilia americana* and *Ostrya virginiana* were scattered or only locally important. *Abies balsamea, Picea glauca, Acer saccharum, Populus tremuloides, Betula papyrifera, Pinus strobus* and *Thuja occidentalis* were the dominant members of the tree canopy, the first 3 exerting the greatest ecologic importance. *Populus tremuloides* and *Betula papyrifera* were important in early successional stages and dominated areas of disturbance. Their appearance in older stands of the spruce-fir type was of a remnant nature with their number and vigor tending to gradually decrease with aging of the community. *Pyrus americana* never occurred with a high importance value although it was present in all stands. The Keweenaw is one of the areas where this species may exist in the community to an extent that it is often included in the quantitative data of the tree layer. It is a characteristic component of the boreal forest on its southern edge, especially in stands along the south shore of Lake Superior from Michigan to Minnesota.

The total list of the 18 tree species may be roughly separated into 2 groups: those which are members of the boreal forest and have their important ecological distribution northward, and those which are members of the deciduous or deciduous-coniferous forests and occur predominantly southward.

The importance values for all tree species in the 4 stands are included in Table I. Data are ordered from left to right on the basis of the moisture characteristic of the stand. *Abies balsamea* and *Picea glauca* have a fairly consistent high representation in all stands, including Silver Creek which was younger and dominated by *Betula papyrifera* and *Populus tremuloides,* and Lake Gratiot which was dominated by *Acer saccharum.* The representation of *Populus tremuloides* and *Betula papyrifera* is interesting. These species with *Abies balsamea* represent a combined importance value of 267 of a possible 300 in the young successional stand (Silver River) and occur in significant amounts in the Delaware and Aetna Creek stands. In the oldest stand, of mixed boreal conifer-hardwoods (Lake Gratiot) only *Betula papyrifera* was present. Data for *Populus* and *Betula* thus point to an important ecological influence in young successional stages following catastrophe and to a gradual disappearance with increasing age of stand. They may be maintained by local disturbance. *Acer saccharum* was present in all stands and in all but one (Delaware) occurred with significant importance. Although *Pinus strobus* might be expected to be relatively more important under dry-mesic conditions or in successional stands (Silver Creek), it had its lowest importance value in this situation but occurred to moderate levels in the other 3 stands. The only other tree species worth mentioning is *Thuja occidentalis.* It was sampled in all stands but attained its greatest influence in wetter situations.

Relationships of tree species in these spruce-fir communities are more clearly understood when data for members of the tree strata are compared with figures on the importance of the same tree species in the tree reproduction layers. Table II shows a comparison of tree and reproduction data on the basis of per cent density. Except in the dense-canopied boreal conifer-hardwood stand (Lake Gratiot), *Abies balsamea* has a higher

TABLE I. The composition of the tree strata of the four stands sampled on the basis of importance values

	Silver River Dry—Mesic	Lake Gratiot Mesic	Delaware Mesic	Aetna Creek Wet—Mesic
Abies balsamea	92.4	89.5	69.2	95.8
Populus tremuloides	92.4		22.6	32.9
Betula papyrifera	82.3	1.0	6.3	1.8
Picea glauca	18.0	55.1	145.9	124.9
Acer saccharum	6.1	122.4	1.0	12.8
Pyrus americana	4.1	3.9	1.0	3.5
Ulmus americana	2.9	1.0		
Acer spicatum	1.8		1.0	1.0
Pinus strobus	1.0	10.9	12.6	17.1
Amelanchier sp.	1.0	1.7	1.0	1.0
Acer rubrum	1.0	1.7	2.7	3.9
Thuja occidentalis	1.0	1.7	20.5	24.8
Tilia americana		1.0		
Ostrya virginiana		1.0		
Betula lutea		4.7		4.7
Quercus rubra		2.1		1.0
Alnus rugosa				1.7
Larix laricina				2.7

TABLE II. Comparison of the tree and sapling data based on per cent density values

	Silver River Dry—Mesic		Lake Gratiot Mesic		Delaware Mesic		Aetna Creek Wet—Mesic	
	Tree	Sapling	Tree	Sapling	Tree	Sapling	Tree	Sapling
Abies balsamea	34.4	67.5	32.5	19.4	31.7	60.8	25.0	43.8
Populus tremuloides	31.2	5.6			6.7		10.0	3.1
Betula papyrifera	25.0	10.6		1.3	1.7		0.6	
Picea glauca	5.0	3.8	14.4	2.5	51.7	12.5	43.7	10.0
Acer saccharum	1.9	1.3	46.3	58.8		4.2	4.4	11.9
Pyrus americana	1.3	0.6	1.3	1.9		3.3	1.3	3.8
Pinus strobus			2.5		2.5	0.8	4.4	
Acer rubrum			0.6	3.8	0.8	5.8	1.3	
Thuja occidentalis		3.8	0.6	1 3	5.0	10.0	7.5	17.5
Betula lutea			0.6				0.6	0.6

representation in the reproduction than in the tree layer. This species can stand heavy litter layers, a situation generally existing in the Great Lakes region, and is quite tolerant. Although heavy reproduction in sapling sizes may not necessarily mean increased representation in future generations, it does indicate that the species has at least the capabilities of maintaining itself under favorable conditions. This is not so with *Picea glauca* since in every case representation in the reproduction layer is reduced by at least 25% and by as much as 83%. It is doubtful that *Picea glauca* will increase in importance in the future to a greater proportion than its present reproduction indicates regardless of how suitable growing conditions may become. *Populus tremuloides* and *Betula papyrifera* are either completely absent in the reproduction or are significantly reduced. Similarly, *Pinus strobus* is almost entirely absent in the reproduction. Only a single sapling of this species was included in the data. *Acer saccharum* presents a completely different relationship. It shows a marked increase in almost all stands except in the young successional type. There is little doubt that it will increase in importance in the tree layer. Reproduction data for *Acer rubrum* indicate a similar increase in importance especially in stands where it is already established. *Thuja occidentalis* shows a significant increase in all stands but especially in wetter situations where vegetative reproduction is profuse.

In Table III the frequency values for seedlings of tree species are presented. These tend to support trends indicated by sapling reproduction values. *Abies balsamea* is again capable of germinating in all types of litter situations but attains lowest frequency values in the predominantly hardwood stand. *Picea glauca* seedlings were conspicuously absent except for very scattered occurrences in the older spruce-fir stand at Delaware. Seedlings of *Populus tremuloides* and *Betula papyrifera* are not considered important in determining reproduction trends since the sapling values are almost completely lacking. *Amelanchier* spp. and *Pyrus americana* are well represented in seedling size classes but tree and sapling data indicate that they rarely attain the tree layer. Seedling data for *Acer saccharum* are remarkably similar to the data for saplings of the species and again indicate increasing numbers in the more mature stands. In the Delaware stand where there were no trees of *Acer saccharum,* saplings were recorded and further increases in the importance of seedlings were shown. *Acer rubrum* is a prolific seeder which germinates under a variety of conditions and is well represented in seedling data.

TABLE III. Frequency values for seedlings of tree species

Species	Silver River DM	Lake Gratiot M	Delaware M	Aetna Creek WM
Abies balsamea	60	45	73	60
Populus tremuloides	20		13	15
Accr spicatum	20		7	10
Acer rubrum	10	35	47	10
Acer saccharum		70	33	15
Amelanchier spp.		25	13	25
Betula lutea		20	7	
Pyrus americana		15	20	20
Ostrya virginiana		15	13	
Prunus virginiana		5	7	10
Betula papyrifera			27	
Picea glauca			7	
Thuja occidentalis			7	
Quercus rubra			7	5

The composition of the stands in terms of shrubs and herbaceous species is presented in Tables IV and V. A comparatively rich shrub and herb flora was present. Twenty-one shrubby species and 98 herbs were recorded in the 4 locations, making a total of 136 species of vascular flora recorded in the upland spruce-fir communities of the peninsula.

There are certain characteristics of occurrence and abundance of these species in the represented stands which are of interest. The values for the total number of species (trees, shrubs, herbs) in each stand vary considerably. Only 52 were recorded in the younger successional stand (Silver Creek) whereas 93, 87 and 95 were recorded in the others. The latter values are quite high when compared with presence lists for other communities, for example, the northern deciduous forest.

Shrub and herb frequencies readily indicate a tendency for certain species to occur more often either in dry, mesic or moist situations. On the other hand these preferences are not displayed in an abrupt manner of occurrence. Species are seldom sharply restricted to specific portions of the moisture series but gradually occur with lesser frequency as situations become less suited to their requirements. These preferences may not be entirely due to gradually changing moisture conditions but may in some way be related to successional changes.

TABLE IV. Shrub species of spruce-fir communities of the Keweenaw Peninsula. Presence and frequency values are presented

Species	PRESENCE				FREQUENCY			
	S.R. DM	L.G. M	D. M	A.C. WM	S.R. DM	L.G. M	D. M	A.C. WM
Arctostaphylos uva-ursi	x				5			
Salix sp.	x							
Shepherdia canadensis	x							
Diervilla lonicera	x	x	x		10			
Lonicera canadensis	x	x	x	x	10	5	20	
Rubus parviflorus	x	x	x	x	25	20	20	5
Rosa sp.	x			x				10
Cornus rugosa	x		x	x				10
Crataegus sp.		x						
Rubus (blackberry)		x				5		
Cornus alternifolia		x	x	x				
Sambucus pubens		x	x					
Ribes triste		x	x	x				10
Rubus idaeus		x	x	x		5	7	5
Prunus virginiana		x	x	x		5	7	10
Corylus cornuta		x	x	x		15		10
Lonicera hirsuta			x				7	
Vaccinium myrtilloides			x					
Vaccinium angustifolium			x	x				5
Alnus rugosa			x	x			7	5
Lonicera dioica				x				

Twenty-five species of shrubs and herbs were present in each of the 4 stands. Of the 25 only 6 had frequency values of 5 or greater in all stands. *Rubus parviflorus* was the only shrub which occurred in quadrats in all 4 stands and *Lonicera canadensis* was the next most important shrub. None of the other shrubs occurred in any stand with a frequency value greater than 15. *Aster macrophyllus, Maianthemum canadense, Mitella nuda, Carex pedunculata,* and *Aralia nudicaulis,*

TABLE V. Presence and frequency values for herbs

Species	PRESENCE				FREQUENCY			
	S.R. DM	L.G. M	D. M	A.C. WM	S.R. DM	L.G. M	D. M	A.C. WM
Monotropa uniflora	x							
Glyceria striata	x							
Cynoglossum officinale	x							
Solidago hispida	x							
Polygala paucifolia	x				5			
Chimaphila umbellata	x		x	x	15			
Corallorhiza maculata	x		x	x				
Geum canadense	x		x	x			5	
Pyrola secunda	x		x	x			7	
Aster macrophyllus	x	x	x	x	90	20	40	50
Linnaea borealis	x	x	x	x	35		7	20
Pteridium aquilinum	x	x	x	x	25		47	25
Maianthemum canadense	x	x	x	x	15	50	67	20
Cornus canadensis	x	x	x	x	15		53	30
Mitella nuda	x	x	x	x	10	5	47	70
Goodyera oblongifolia	x	x	x	x	10			
Carex pedunculata	x	x	x	x	5	40	80	60
Aralia nudicaulis	x	x	x	x	5	5	20	20
Osmorhiza claytoni	x	x	x	x	5	10		5
Viola conspersa	x	x	x	x	5	5		20
Viola incognita	x	x	x	x		75	53	30
Oryzopsis asperifolia	x	x	x	x		30		15
Galium triflorum	x	x	x	x		25	53	25
Dryopteris spinulosa	x	x	x	x		15	13	25
Hepatica americana	x	x	x	x		5	33	10
Athyrium filix-femina	x	x	x	x		5	7	
Dryopteris disjuncta	x	x	x	x			7	10
Circaea alpina	x	x	x	x			7	5
Botrychium virginianum	x	x	x	x				20
Actaea rubra	x	x	x	x				10
Carex intumescens	x	x	x	x				5
Viola selkirkii	x	x	x	x				
Agrimonia gryposepala		x						
Aralia racemosa		x						
Botrychium matricariaefolium		x						
Carex brunnescens		x						
Epilobium glandulosum		x						
Galium asprellum		x						
Lactuca canadensis		x						
Lycopodium complanatum		x						
Lycopodium obscurum		x						
Carex crinita		x						
Uvularia sessilifolia		x						
Botrychium multifidum		x				5		
Pteretis pensylvanica		x				5		
Milium effusum		x				10		
Apocynum androsaemifolium		x	x					
Epilobium angustifolium		x	x					
Osmunda claytoniana		x	x				7	
Mitchella repens		x	x				20	
Anemone quinquefolia		x	x			5	20	
Carex pensylvanica		x	x			15	27	
Solidago flexicaulis		x		x		5		
Trillium cernuum		x		x		5		
Sanicula marilandica		x		x		10		10
Lycopodium clavatum		x		x		30		5
Mertensia paniculata		x		x				30
Geranium bicknelli		x		x				
Pyrola elliptica		x	x	x			7	
Satureja vulgaris		x	x	x			7	
Equisetum sylvaticum		x	x	x		5		
Lycopodium lucidulum		x	x	x		5	7	
Coptis groenlandicum		x	x	x		5	20	
Streptopus roseus		x	x	x		5	13	5
Anaphalis margaritacea		x	x	x		7		
Lycopodium annotinum		x	x	x		10	20	
Trientalis borealis		x	x	x		10	20	15
Viola pubescens		x	x	x		20		
Viola renifolia		x	x	x		20	13	5
Carex arctata		x	x	x		20	33	15
Brachyelytrum erectum		x	x	x		25	33	10

(Table V. Continued)

Species	Presence				Frequency			
	S.R. DM	L.G. M	D. M	A.C. WM	S.R. DM	L.G. M	D. M	A.C. WM
Rubus pubescens		x	x	x		25	53	65
Clintonia borealis		x	x	x		35	33	
Aster lateriflorus		x	x	x			47	15
Prunella vulgaris		x	x	x			7	10
Fragaria virginiana		x	x	x			13	5
Equisetum arvense		x	x	x			7	5
Aster umbellatus		x	x	x				5
Geum aleppicum			x					
Goodyera repens			x					
Prenanthes alba			x					
Epigaea repens			x				13	
Antennaria sp.			x	x				
Hieracium scabrum			x	x				
Achillea millefolium			x	x				5
Gaultheria hispidula			x	x				5
Petasites palmatus			x	x			7	10
Moneses uniflora			x	x			13	5
Caulophyllum thalictroides				x				
Carex canescens				x				
Equisetum scirpoides				x				
Habenaria hyperborea				x				
Heuchera richardsonii				x				
Hieracium aurantiacum				x				
Anemone canadensis				x				5
Cynoglossum boreale				x				5
Melampyrum lineare				x				5
Cystopteris bulbifera				x				5
Total species present	52	93	87	95				

were the 5 herbs which occurred in the frequency data for all stands. Examination of Tables IV and V indicates the shrub and herb floras of these spruce-fir communities are composed of a mixture of species, some of which attain their ecological optima farther south in the deciduous forest (*Cornus rugosa, Geum canadense, Aralia racemosa, Solidago flexicaulis, Prenanthes alba, Caulophyllum thalictroides, Heuchera richardsonii, Anemone canadensis,* etc.) and others which occur with greater frequency northward in the boreal forest (*Shepherdia canadensis, Ribes triste, Linnaea borealis, Cornus canadensis, Mitella nuda, Pyrola secunda, Lycopodium clavatum, L. annotinum, Trientalis borealis, Petasites palmatus,* etc.).

Discussion

When the composition of the individual stands in terms of dominant tree species is considered (Table I) it is clear that they are predominantly boreal in character. In the stand at Delaware, *Abies balsamea* and *Picea glauca* have a combined ecological importance value of 215 (of a possible 300), and the important associated tree species all occur well within the main mass of the boreal forest farther north in Canada. The combined importance values for these 2 important boreal dominants are 110, 145 and 221 respectively in the 3 other stands. *Acer saccharum, Betula lutea* and *Acer rubrum* are dominants of the deciduous forest and their combined importance values in the stands are 7, 129, 4 and 21. It is thus evident that even in situations highly favorable to the establishment and development of spruce-fir forest, total purity of these species and their usual associates is probably not often attained. Evidence of sapling and seedling regeneration further emphasizes that purity of composition would not be continuously maintained. As the community matures and the site factors approach mesic conditions, the possibility of the invasion of deciduous forest elements in increasing amounts is imminent. The complete dominance of the deciduous species may be prevented in certain situations under the influence of local climate or disturbance which may permit the conifers to survive. Thus deciduous stands in the area in which old hardwoods are overtopped by *Abies balsamea* and *Picea glauca* point to the gradual encroachment by hardwoods and yet the abundant reproduction of spruce and fir in the mature stand of spruce-fir at Delaware points to a long occupancy of this type. Curtis (1959) believes the same trends are evident in spruce-fir communities in northern Wisconsin and adjacent Michigan but yet conjectures the possibility of a slight shift in climate that might permit the spruces and firs to long retain their influence.

Thus an intermixing of elements of the deciduous and spruce-fir forests characterizes the patterns of forest development in this area. Each community will show trends toward purity where environmental and biotic factors permit this to occur. Once relative stability has been attained, stands composed predominantly of deciduous elements probably have greater endurance qualities than those predominantly of spruce-fir. The evidence of stand composition in terms of trees, saplings and seedlings indicates that the spruce-fir communities of the Keweenaw possess successional traits, although long continued occupancy may occur in certain environmental situations or with continued disturbances. Long-lived stands in the absence of disturbance tend to become increasingly dominated by *Abies balsamea* and be invaded by deciduous species.

Data on tree composition indicate that *Picea glauca* may not be as important as *Abies balsamea* in the tree layer in some stands (Silver River, Lake Gratiot) but in others it may occur with greater importance even to twice the importance value of *Abies* (Delaware, Aetna Creek). In stands of this community throughout the Lake region (Maycock and Curtis 1960) a similar relationship between these species prevailed. In 103 stands, containing both species, *Abies* had a greater importance value than *Picea* in 69 stands and the reverse was true of the other 34 stands. There is thus no evidence that *Abies balsamea* is consistently the leading dominant to the extent that an *Abies-Picea* community (Buell and Niering 1957) has any more significance than a *Picea-Abies* community except as the existing sequence of leading dominants in certain localities or ecological sites.

The tree data also show that certain trees are sensitive to characteristics of site moisture and attain greater importance in such situations. Similar and perhaps more marked moisture preferences are shown by the shrubs and herbs. Groups of species attain highest importance in certain moisture conditions and decrease in others. The data for *Streptopus roseus, Rubus pubescens, Fragaria virginiana, Carex pedunculata* and *Mitella nuda* emphasize these continuous responses of species to moisture.

One of the striking characteristics of these communities is the high number of species per stand (Table V). Maycock and Curtis (1960), working in stands of this type recorded an average of 67 trees, herbs and shrubs per stand in a total of 110 stands in the Great Lakes region. The average for the 4 Keweenaw stands is 82, an increase of approximately 20%. This wealth in species is partly due to the mingling of plants representative of 2 formations and to the central position of the Keweenaw in a region where many east-west distributions begin and end, but such factors similarly affected the results of the previous study. This marked increase in the average number of species per stand is best accounted for by favorable environmental conditions and the moderating effect of the lake waters on climate to produce considerably cooler summer temperatures which permit the boreal species to become established and at the same time are not unfavorable to the deciduous forest herbs.

These moderated climatic influences produced by Lake Superior are probably the best explanation for the existence of these southern outliers of the boreal forest. A persistent layer of deep snow that remains late in the spring, the cooling effects of winds from the lake in summer and a reversal of this trend in the winter, the lack of climatic extremes of short duration brought about also by this moderation, and all of these producing a shorter growing season, seem to combine to favor the persistence of these local pockets of spruce-fir vegetation.

These forests possess structural characteristics which relate them to a more extensive vegetational complex which occurs throughout the Great Lakes region. This complex incorporates the ecological characteristics and species components of the boreal and deciduous forests and is transitional and continuous in nature. The attributes of either community type tend to be balanced or to predominate depending on local environmental circumstances. The Keweenaw peninsula, because of its peculiar geographical position, its variable topography and its unique ecological situation, provides this variety of environmental circumstances.

SUMMARY

Four stands typical of the boreal forest communities of the northern extremity of the Keweenaw peninsula in northern Michigan were studied during the summer of 1955. Quantitative data were collected using the quarter method to provide importance values for tree species and frequencies of herbs and shrubs.

The quantitative values for different plants coincided with site moisture conditions and it appears that moisture differences are the factors mainly responsible for the continuous variation in composition which exists. Related to moisture effects are successional tendencies which point to eventual invasion of deciduous forest in the absence of disturbance. Long term occupancy of boreal forest may be possible in favorable microclimatic situations or in areas where local natural disturbances are prevalent.

These communities on the southern fringe of the boreal forest form a small portion of a more extensive continuum throughout the northern Great Lakes region.

REFERENCES

Braun, E. L. 1950. Deciduous forests of eastern North America. Blakiston, Philadelphia. 596 pp.

Buell, M. F. and W. A. Niering. 1957. Fir-spruce-birch forest in northern Minnesota. Ecology **38:** 602-610.

Cottam, G. and J. T. Curtis. 1956. The use of distance methods in phytosociological sampling. Ecology **37:** 451-460.

Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, 657 pp.

Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology **32:** 476-496.

Cunningham, R. N. and H. G. White. 1941. Forest resources of the upper peninsula of Michigan. U.S.D.A. Misc. Publ. **429:** 1-32.

Fernald, M. L. 1935. Critical plants of the upper Great Lakes region of Ontario and Michigan. Rhodora **37:** 197-222, 238-262, 272-301, 324-341.

Fernald, M. L. 1950. Gray's Manual of Botany. Amer. Book Co., New York, 8th ed. 1632 pp.

Fuller, A. M. 1950. The Ridges Wildflower Sanctuary at Bailey's Harbor, Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. **40:** 149-157.

Klugh, A. B. 1912. Plant formations of the Bruce Peninsula. Ont. Nat. Sci. Bull. **7**: 10-21.

Maycock, P. F. and J. T. Curtis. 1960. The phytosociology of boreal conifer-hardwood forests of the Great Lakes region. Ecological Monog. **30**: 1-35.

Nichols, G. E. 1935. The hemlock-white pine-northern hardwood region of eastern North America. Ecology **16**: 403-420.

Shantz, H. L. and R. Zon. 1924. The physical basis of agriculture: Natural Vegetation. In Atlas of American Agriculture (Pt. 1, Sect. E., 29 pp.) Washington, D. C., U.S.D.A.

Steere, W. C. 1937. Critical bryophytes from the Keweenaw peninsula, Michigan. Rhodora **39**: 1-14, 33-46.

———, 1938. Critical bryophytes from the Keweenaw peninsula II. Annal. Bryol. **11**: 145-152.

Thomson, J. W. 1951. Some lichens from the Keweenaw peninsula, Michigan. Bryol. **54**: 17-53.

United States Department of Agriculture. Yearbook for 1941, Climate and Man. Washington, D. C. 1248 pp.

Van Hise, C. R. and C. K. Leith. 1911. The geology of the Lake Superior region. U. S. Geol. Surv. Manual **52**: 651 pp.

Van Pelt, J. R. 1949. Boston and Keweenaw. Amer. Scientist **37**: 219-234.

Weaver, J. E. and F. E. Clements. 1938. Plant Ecology. McGraw Hill, New York. 601 pp.

FLOWERING AND FRUITING IN THE WHITE OAKS. I. STAMINATE FLOWERING THROUGH POLLEN DISPERSAL[1]

Ward M. Sharp and Henry H. Chisman

The Pennsylvania Cooperative Wildlife Research Unit and the Department of Forest Management, Pennsylvania State University, University Park, Pennsylvania

Introduction

White oak acorns are a choice food for forest game but their year-to-year production has been unpredictable. Several untested hypotheses such as the effects of heavy rains and prolonged wet spells on pollen dispersal, nutritional deficiencies, droughty summers, and late spring frosts have been stated and generally accepted as the causes of poor acorn years. From April 1949 through 1960, a study of flowering and fruiting in the white oaks was carried on in central Pennsylvania to determine factors influencing acorn production and to test existing hypotheses regarding the causes of good and poor acorn yields.

This is a report of a study on the catkin or male flowers. Acorn development will be described in a subsequent paper.

The objectives of this study were to observe:

(1) The staminate catkin with regard to its emergence, early growth and maturation; the progression of pollen shedding over the crown of the tree; and the effects of wind movement and humidity on pollen dispersal.

(2) The environmental factors favorable or unfavorable to pollen development and shedding such as tolerance of catkins to frost intensity, effects of prolonged, rainy periods and extended periods of dry atmospheric conditions.

(3) The relationship between new shoot elongation and leaf blade expansion during flowering and following pollen dispersal.

The Study Area

Flowering and fruiting in the white oaks were studied in northern Huntingdon and central Centre Counties, Pennsylvania, along a transect traversing the Ridge and Valley Province and extending northwestward upon the edge of the Allegheny Plateau (Fenneman 1938). This transect begins at Masseyburg near Route 545 in Huntingdon County. It follows this route to State College, and then extends northwest along or near Route 322 to approximately 12 miles northwest of Port Matilda, Pennsylvania. Sites were selected along this transect for year-to-year observations.

The transect crosses 3 valleys and 2 mountain ranges within the northern Ridge and Valley Province, namely, the Stone, Nittany, and Bald Eagle Valleys; and the Tussey and Bald Eagle Ranges. Leaving the Ridge and Valley Province the transect extends northwestward upon the Allegheny Plateau which, at this location, is known as the Allegheny Front. The terrain along this route is diverse, with a wide range of altitudes, soil types, and physiographic aspects.

Procedure

The procedure was (1) to study flowering on trees within a number of selected sites; (2) to study flowering on selected trees where branches were marked with numbered metal tags; and (3) to follow development of catkins through pollen dispersal, shoot elongation, growth of the female flowers, and leaf blade expansion through anthesis.

---

[1] Paper No. 103 of the Pennsylvania Cooperative Wildlife Research Unit, jointly sponsored by the U. S. Fish and Wildlife Service (Department of the Interior), Pennsylvania Game Commission, the Pennsylvania State University, and the Wildlife Management Institute.

A number of sites were selected on which trees of a single species were marked for future observation. Ten sites were selected for white oak (*Quercus alba* L.), 5 for chestnut oak (*Q. prinus* L.), 5 for scrub chestnut oak (*Q. prinoides* Willd.), and one for burr oak (*Q. macrocarpa* Michx.). The burr oak is uncommon in the region, accounting for its single location. All tree locations were recorded on a map. Trees were selected within each site. Five to 10 branches on each tree were marked with metal tags which were numbered in sequence for each tree.

All trees were studied from the ground with 7 × 50 binoculars. The crowns were observed 2 to 3 times each week from the time of bud swelling through catkin emergence and development.

Tagged branches were closely observed for flower growth, leaf blade expansion, pollen dissemination, and to follow the progress of catkin ripening and pollen dissemination. At the time of pollen shedding, observations were made twice daily.

Weather data were obtained from the U.S.D.A. Pasture Laboratory which has maintained complete 24 hr records since January 1949. Seven of the white oak sites lie within ¼ mile to 6 miles of this laboratory which is at the edge of the University farms of the Pennsylvania State University. The weather data for periods of pollen dispersal have been correlated with the data maintained at this central station. Maximum-minimum thermometers were also used to test temperature stratification at various altitudes.

Catkin Development, Pollen Shedding, Lag in Leaf Blade Expansion, and Flowering Waves

The Staminate Catkin

The development of the male flower or catkin in the white oaks has received little attention in the literature. Rendle (1925) and Busgen and Munch (1929) refer to the solitary male flowers in the birches, alders, hazels, and oaks. Rendle stated that the male flowers or catkins in North American oaks are odorless and insects are not attracted to them. Wind and air currents are the only means of transporting pollen to the female flower in *Quercus* and the pendant nature of the catkins facilitates their mobility, thus aiding in wind dissemination of the pollen (Rendle and Busgen & Munch, *op. cit.*). Asa Gray (1879) was one of the earlier workers who referred to the male flowers as aments or catkins, and forest trees and shrubs bearing this type of male flower were called *"amentaceous."*

A commonly accepted assumption is that the species of white oaks are cyclic or periodic with acorn crops occurring on a 3 to 5 yr basis. In forest trees which are known to be periodic, flowers are produced only in irregular years. The sugar maple (*Acer saccharum* Marsh.) is believed to be a typical periodic or cyclic producer of a seed crop. It produces flowers only at 3 to 4 yr intervals. In this 12 yr study, all white oak trees selected on the 10 sites produced a good to heavy crop of male flowers each year. Female or pistillate flowers were also produced each year. Random observations of many trees outside the sites along the transect always revealed an occasional tree that produced no flowers. Those under 10 in. dbh were believed not to have attained flowering or fruiting age. The periodic occurrence of a white oak acorn crop is not due to periodic flowering.

Emergence and Early Development.—The staminate catkins are the first green shoots to appear with the opening of the winter buds on the oaks. They grow from the base of the inner scales of the clustered buds at the apex of the woody twigs of the previous year's growth. Their emergence and growth follow a similar phenological sequence in the white, chestnut, burr, and scrub chestnut oaks. Records of these species for several seasons revealed that the catkins emerged from April 30 to May 9. *Q. alba* was the only exception, having both early and late flowering trees. The early flowering trees coincided with other species of white oaks, but catkins emerging in the late flowering trees in the same locality were as late as May 19.

The first catkins appear in the topmost branches. A rapid downward progression of emergence follows so that those on the lowermost branches are the last to appear. Catkins are grouped in clusters ranging from 3 to 10 or more per twig tip. The abundance of catkins on a tree was recorded as 3+, 5+, or 10+ per shoot tip, and a shoot tip bearing 10 to 12 catkins was classed as 10+. Each year an individual tree was always uniform in the abundance of catkins produced. For example, a tree bearing 3+ catkins (2 to 4 per shoot tip) rarely exceeded this number over the entire crown. This method was used in determining and recording catkin abundance. This study did not show that there was a correlation between catkin abundance, female flowers, and acorn production in the white oaks in any season.

Stalk or Rachis Elongation and Maturation of Catkins.—The catkins are erect and dense shortly after emerging from the bud (Fig. 1a). The central axis or rachis of these floral structures elongates gradually, becoming semipendent 2 to 8 days following emergence (Fig. 1b), and pendent 5 to 12 days after its first appearance (Fig. 1c). These structures were completely elongated and anthesis was completed in the white oaks 11 to 16 days following their emergence from the bud (Fig. 1d). Cell enlargement and differentiation occurred acropetally in the rachis of the catkin and the apical portions matured several days after the basal portion.

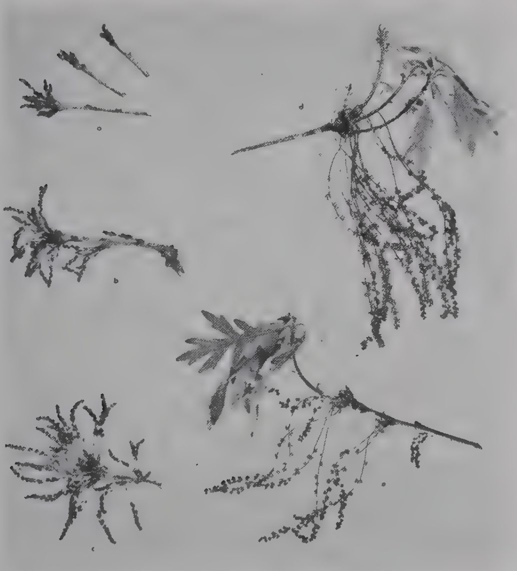

Fig. 1. Stages in catkin development of white oak, *Q. alba:* (a) catkins *emerging;* (b) catkins *erect* to *semipendent;* (c) catkin appearance when *semipendent;* (d) catkins *elongated* and anthers ripened; and (e) catkins with anthers at stage of pollen dispersal. Note the lag in leaf growth up to this time.

The number of days for complete catkin elongation, anther development, and ripening of pollen was never uniform from one year to the next (Table I). This annual variation—in the individual tree—was closely associated with the weather, particularly with air temperatures prevailing during anthesis. Cloudy, cool periods caused an apparent cessation when no appreciable growth changes could be detected in the catkins. Warm weather produced a marked acceleration in growth. This effect of warmth on growth was noteworthy in May 1953 when high temperatures prevailed. Information obtained during 1949-59 indicated that growth in catkins was greatest when night temperatures were above 50°F.

On white oak-1d (Table I), an early flowering tree, catkins emerged on May 5 in 1951, 1952, and 1953. The time needed to complete pollen shedding was 15, 19, and 11 days, respectively. Late flowering white oak-1a during the same years dispersed pollen 11, 14, and 13 days following the emergence of catkins. High temperature after the middle of May was probably the chief factor in the shorter period of anthesis. The average time for catkin emergence to completion of pollen shedding in 4 species of white oaks was 15.5 days (1950-52), and 10.6 days for 1953.

Pollen Shedding in the White Oaks

Catkins on the topmost branches were the first to shed pollen. The dehiscing of anthers in the catkins progressed downward so that those on the lowest branches were the last to lose their pollen. This pattern follows that of anther emergence; but trees in open fields often proved an exception to the above rule during dry, sunny, windy weather.

Anthers dehisce acropetally; those at the base of the catkin open first, and there is a gradual dehiscence toward the apex. The basal third of a catkin may disperse pollen one day and the apical portions shed their pollen during the second or third day following.

Catkin maturity is recognized by the yellowish-green color and noticeable turgidity of the anthers. When weather conditions were favorable, the day of pollen dissemination could be predicted. Increasing cloudiness and humidity followed by rain at this time would delay pollen shedding in the ripened catkins until the first warm sunny day following the storm.

Pollen shedding could be expected soon after the catkins had become 80-90% elongated. The absolute length of the catkin was not a reliable criterion in predicting pollen shedding. On some white oaks, catkins only 7 cm long dispersed their pollen while in others dispersal was delayed until catkins were 11 to 14 cm long. Catkins in the scrub chestnut oak were 6 to 8 cm long when their pollen was shed.

Lag in Leaf Blade Expansion During Anthesis

New, unfolded leaves appeared on the shoots of the current season about the time that the catkins became semipendent. In those oaks producing a crop of catkins, there was a definite lag in leaf blade expansion as long as the catkins contained pollen. Leaf measurements from several trees over several years revealed that the distal blade length of the white oak averaged 5 cm while those of the chestnut oak averaged 7 cm at time of pollen shedding. When pollen was dispersed from a tree there was a rapid spurt in leaf growth, and by the following day the leaf area had increased 50%.

TABLE I. Developmental stages of the staminate catkins and leaves during anthesis in three species of white oaks

Species	Year	Date Catkins Emerged	Date Catkins Semi-pendent	Date Leaves Unfolded	Date Catkins Pendent	Catkins 60-80% Elongated	Date Pollen Shedding	Leaf Size at Pollen Shedding	Total Days for Catkin Anthesis
White oak, 1a........	1950	5–19–50	5–22–50 (3 da)	5–22–50	5–25–50 (3 da)	5–28–50 (3 da)	5–30–50 (2 da)	3–9 cm	11
" " "	1951	5–16–51	5–18–51 (2 da)	5–18–51	5–21–51 (3 da)	5–24–51 (3 da)	5–27–51 (3 da)	7–10 cm	11
" " "	1952	5–13–52	5–15–52 (2 da)	5–15–52	5–19–52 (4 da)	5–26–52 (7 da)	5–27–52 (1 da)	7 cm	14
" " "	1953	5–10–53	5–12–53 (3 da)	5–12–53	5–18–53 (6 da)	5–20–53 (2 da)	5–24–53 (4 da)	—	13
White oak, 1d........	1950	5–9–50	5–12–50 (4 da)	—	5–16–50 (4 da)	5–20–50 (4 da)	5–26–50 (6 da)	—	18
" " "	1951	5–5–51	5–12–51 (8 da)	—	5–14–51 (2 da)	5–18–51 (4 da)	—	—	—
" " "	1952	5–5–52	5–8–52 (4 da)	5–8–52	5–13–52 (5 da)	5–15–52 (2 da)	5–23–52 (8 da)	5-7 cm	19
" " "	1953	5–5–53	5–7–53 (3 da)	5–7–53	5–9–53 (2 da)	5–12–53 (3 da)	5–16–53 (4 da)	—	12
Chestnut Oak........	1950	5–5–50	5–7–50 (3 da)	5–7–50	5–9–50 (2 da)	5–16–50 (7 da)	5–19–50 (3 da)	7-9 cm	15
" "	1951	5–1–51	5–3–51 (3 da)	5–3–51	5–5–51 (2 da)	5–9–51 (4 da)	5–15–51 (6 da)	10-11 cm	15
" "	1953	5–3–53	—	—	—	5–8–53	5–10–53	—	—
Scrub Chestnut Oak...	1949	5–3–49	5–9–49 (7 da)	—	5–12–49 (3 da)	—	5–19–49 (7 da)	4-5 cm	17
" " " ...	1951	5–1–51	5–8–51 (8 da)	5–8–51	5–12–51 (4 da)	5–16–51 (4 da)	5–18–51 (2 da)	6-8 cm	18
" " " ...	1952	4–29–52	5–5–52 (7 da)	5–5–52	5–7–52 (2 da)	5–15–52 (8 da)	5–18–52 (3 da)	4-5 cm	20

This was characteristic of all species of the white oaks. It was possible to determine those trees which had shed their pollen by the increased growth within the leafy canopy.

The reason for a lag in leaf expansion prior to pollen dispersal may rest in some aspect of physiology. Arrested leaf expansion appears to facilitate pollen dispersal. A rapidly developing leafy canopy would screen pollen from reaching the stigmas of the female flowers.

Flowering Waves and Periodicity in the White Oaks

The chestnut and scrub chestnut oaks displayed no noticeable seasonal variation in time of catkin emergence except in cases of differences in altitude or in frost pocket areas. The white oak, on the other hand, displayed a distinct variation which is termed *flowering waves.* These differences in time of catkin emergence varied in individual trees on the same site. For this reason, consistent seasonal variations could not be attributed to differences in temperatures or other external site factors. The difference could be more properly assigned to genetic idiosyncrasies.

Individual white oak trees could be classed as early, intermediate, or late flowering. Trees characteristically early, medium or late flowering were studied for 12 yrs. The late flowering white oaks, for example, put forth catkins on May 13 in 1952 to as late as May 19 in 1950. The earliest flowering trees put forth catkins on May 5 in 1952 and on May 11 in 1950. The spring of 1950 was unseasonably late while 1952 was normal.

INFLUENCE OF RAINFALL, PREVAILING TEMPERATURES, WINDS, DRY ATMOSPHERIC CONDITIONS, AND FROSTS ON POLLEN DEVELOPMENT AND DISPERSAL

Catkin Emergence in Relation to Air Temperatures

The bursting of flower buds and emerging of catkins in white oaks could be expected to advance when temperatures above a minimum of 50°F persisted over 10 days. Swelling and opening of the flower buds during warm weather in late April was slower in the white oaks than in the black oaks. Catkins emerged in the red, scarlet, and black oaks following the first warm days in late April, and pollen dispersal was already completed by the time catkins in the white oaks were emerging or becoming semipendent.

Catkin emergence in the oaks was delayed as the altitude increased. In undulating hills of the lowlands there was no noticeable lag in bud bursting on either north- or south-facing terrain as long as the altitude remained constant. Emergence on a study site of chestnut oaks, on the narrow crest of Tussey mountain on Route 545 at 2061 ft, was about 5 days later than that of chestnut oaks on the lower south slope at 1100 ft. But along the front of the broad Allegheny Plateau on the northern end of the study transect where the altitude ranged from 2164-2171 ft, and where the influence of this high land mass affected meteorological conditions, white and chestnut oaks were consistently 10-12 days later than those in the lower Ridge and Valley Province.

A few unseasonably warm spring days forces buds to open in some species of forest trees although there may have been relatively little change in soil temperature. The aspens respond quickly to an increase in air temperatures while soil temperatures are relatively unchanged. The senior author has observed quaking aspens (*Populus tremuloides* Michx.) to put forth catkins in the Rocky Mountain region of Montana when the winter's accumulation of snow was in evidence everywhere except for small, circular bare spots about 5 ft in diameter immediately surrounding the bases of the trees. The oaks respond to warm air currents, the species of black oaks responding earlier than the white oaks by almost a week. April, 1952, was consistently cooler than in the 3 previous years, but late in that month the weather became unseasonably warm and catkin emergence was on schedule with previous years.

Weather Conditions Conducive to Pollen Dispersal

Weather conditions prevailing during periods of optimum anther dehiscing and pollen shedding were recorded and studied to determine the optimum conditions under which this process occurred. The relative humidity and air temperatures on clear, sunny days were the controlling factors. Light breezes hastened the process.

Pollen dispersal in ripened catkins occurred when the relative humidity dropped and remained below 45% for several hours. The ripened catkins of scrub chestnut oak dispersed pollen within a few hours on warm sunny days when the relative humidity dropped from 45 to 35% with an air temperature ranging from 63°-69°F (Fig. 2). White oaks and chestnut oaks responded more slowly, often requiring 3 days in the former to 2 days in the latter to complete pollen shedding, when the relative humidity dropped below 45% (Figs. 3 and 4).

White oak 1c on Site No. 1 represents an example of the effect of humidity on anther dehiscence. The relative humidity for May 18, 19, 21, 22, and 23, 1952, is graphed for this tree in Figure 3. May 20 was not graphed because rainfall during the day prevented the relative humidity from dropping below 90%.

On May 18 the relative humidity dropped below 45% for 3 hrs from 2-5 pm. None of the ripened anthers had opened on white oak 1c, but the ripened anthers in scrub chestnut oak No. 1 R.P. dispersed pollen during this brief period. Air temperatures from 2-5 pm ranged between 63° and 69°F (Fig. 3). Relative humidity remained below 45% for 5 hrs on May 22 and 6½ hrs on May 23 (Fig. 3). Pollen dispersal was completed on tree 1c during these periods. Air temperatures during pollen dispersal in this white oak ranged between 67° and 79°F.

Effects of Rainy, Wet Periods on Pollen Dispersal

Prolonged rainfall during the period of pollen dispersal has been cited as a possible cause of acorn failure. Baker (1950) believed that long protracted rains interfered with pollen dispersal to the female flowers of those forest trees which are wind-pollinated. Strong evidence was found by Boyd and Latimer (1933) that heavy rains did not wash pollen from the stigmas of McIntosh apples in a quantity sufficient to prevent a satisfactory fruit set. Our studies revealed that in the white oaks the ripened anther sacs act hygroscopically, remaining closed when the relative humidity is above 45%, opening when it drops below 45%. Dorsey (1919) found that opened anthers in plums would close within 2-3 min when exposed to water. He also found that prolonged rain did not burst pollen or kill it and that rain did not wash pollen from the stigmas.

Showers occurring on one or two consecutive days were frequent during the study, but heavy

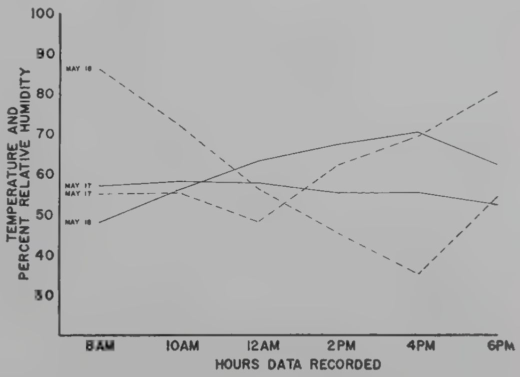

FIG. 2. The ripened catkins of scrub chestnut oak will disperse pollen within a few hours. Pollen shedding from ripened catkins did not occur on May 17, 1952, when the relative humidity, except for a brief period at noon, remained above 50. But when the relative humidity dropped below 45% from 2 to 5 pm on May 18, pollen shedding was completed. *Solid lines* represent the temperature while the *broken lines* represent the relative humidity.

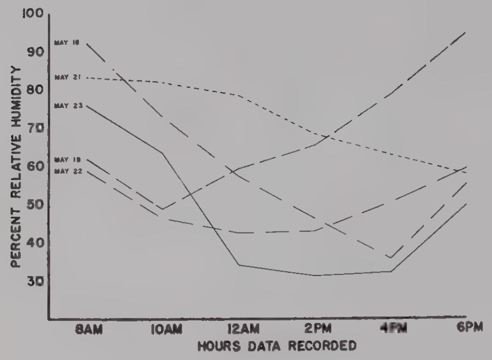

FIG. 3. Catkins in white oak 1c were fully ripened for pollen dispersal on May 18, 1952, but rain during May 18-21 prevented pollen shedding. Pollen shedding occurred on May 22 and 23 when the weather cleared and the relative humidity dropped below 45%.

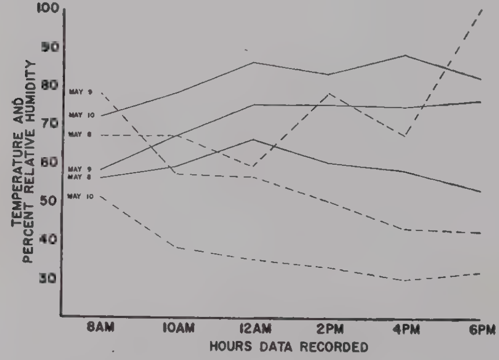

FIG. 4. The effects of relative humidity on pollen shedding in a chestnut oak. The *solid lines* represent the temperature and the *broken lines* represent the relative humidity from 8:00 am to 6:00 pm on May 8, 9, and 10, 1953. Catkins were fully ripened on May 8, but atmospheric moisture conditions were unfavorable for anther dehiscence. Pollen shedding started on May 9 when the relative humidity dropped below 45% and was completed on May 10.

downpours did not wash out the pollen. One prolonged rainy siege occurred from May 15-21, 1952. Pollen dissemination was retarded beyond the normal after-ripening period on a few of the trees under study. Over-ripened catkins dropped intact with the anthers filled with pollen.

The dropping of catkins containing pollen was demonstrated at Site 1, located on the farms of the Pennsylvania State University (Fig. 3). White oak tree 1c contained fully ripened catkins on May 17. Had May 18 been clear and warm, pollen shedding would have occurred, but wet rainy weather continued until May 22. Many catkins dropped to the ground on May 21, and approximately 50% of the catkin crop had dropped from this tree by nighttime. These contained yellowish-green anthers which were turgid and filled with pollen. Several catkins placed in a warm dry room discharged all pollen within an hour. The weather cleared considerably on May 22, and on May 23 the aments remaining on the tree dispersed their pollen within a few hours. All other trees on this site had shed their pollen prior to May 18. White oak 1c was the only tree on this site which produced acorns the following fall—a light crop—but the only crop produced by this tree during 5 consecutive years of observations.

Effects of Wind in Normal, Wet, or Droughty Seasons

A light wind (5-8 miles per hour) on warm, dry, sunny days accelerated pollen shedding in the ripened catkins. Stronger winds during May, when rains were frequent, were accompanied by cloudiness, lowered temperatures, and an increased moisture content of the atmosphere. High winds under these conditions did not influence pollen dispersal. Pollen shedding did not occur when the relative humidity was 50% or higher.

A moderate, warm, dry wind on sunny days hastened shedding of pollen on the windward side of trees several hours prior to complete pollen dispersal from the leeward side. The following is cited as a typical example of a white oak tree in an open field. This white oak was inspected at 7:30 am on May 25, 1950. Pollen shedding was 25-30% completed on the terminal portions of the crown. The following day was warm and sunny with a moderate, dry, southeast wind. The tree was inspected at 5:00 pm for pollen dispersal. The catkins on the windward side of the crown had lost 80% of their pollen while those on the leeward side had dispersed only 40%. Pollen was completely shed on the southeast side at 6:00 pm on May 26. The catkins on the leeward side had dispersed 60-70% of their pollen during the same time. The weather was similar on both days, but the wind had subsided to a light southeast breeze during the second day. Pollen shedding was completed on the northwest or leeward side prior to 4:00 pm of May 27.

Drought has been generally accepted as a cause in the reduction of acorn yields. Baker (1950) believed that the failure of fruit set was caused by drought, but he made no inference regarding its effects on the male flowers which produce the pollen. He stated that periods of drought, when accompanied by parching winds, may cause immature fruits to drop. Baldwin (1942) believed that dry, somewhat windy weather in the season of pollen dispersal promoted pollination, but gave no facts to substantiate or clarify this statement. No reference citing evidence on the effects of drought or very dry atmospheric conditions on the male flowers was found in the literature. In early May, 1955, when male flowers (catkins) were emerging and developing in the white oaks, it was observed that the desiccating, windy weather prevailing prior to pollen ripening was detrimental. The immature catkins, containing unripened pollen, desiccated and when the relative humidity dropped to as low as 22% on May 5, 1955, and the temperature rose to 84°F the anthers dehisced and lost their immature pollen. At the time this pollen was shed, the female flowers were undeveloped and unreceptive to pollen. The catkins in the chestnut oaks were the least tolerant to these conditions, although all species were affected to some degree.

In flowering periods, when there was a normal amount of rainfall and atmospheric moisture, the shelter of the surrounding forest canopy acted as a windbreak and minimized the influence of wind on the ripening catkins. Pollen shedding began in the upper crowns and progressed downward, the lower branches shedding pollen 2 or 3 days later, corresponding to the phenological timetable in earlier development of the catkins. But in lone trees in fields, wind influenced all catkins on the windward side to disperse their pollen at an equal rate while pollen shedding on the leeward side of the crown was delayed until the second and third day. Catkins on the lower branches of open-grown trees were forced by the moderate winds to shed pollen a few days earlier than would have occurred normally had the weather been calm. The canopy of the forest offered little protection in rainless periods with very dry atmospheric conditions and strong winds—the type of weather which creates fire hazard conditions in May.

Influence of Frosts on Flowering in the White Oaks

Frosts occur during the growing season when night temperatures drop below the freezing point in a particular area (Geiger 1950). Haynes (1947) classes frosts according to intensity as light, heavy, and killing. Killing frosts sear the green leaves, shoots, and flowers on a majority of trees and shrubs in an area. The resulting brown, seared, forest canopy is referred to as the result of a "black freeze." Light to heavy frosts do not sear the leaves or tender, succulent shoots although flowers may be damaged.

The white oaks are not visibly damaged by either light or heavy frosts; only the "black freezes" are obviously detrimental to the new leaves, shoots, and flowers. Heavy frosts which approach the lower limits of a killing frost may injure the flowers in the white oaks although no visible damage is apparent.

The accepted belief that frosts may be a limiting factor in the production of white oak acorns was not confirmed by studies of the male flowers. From May, 1949, through May, 1943, there were no frosts in the study area, except on 2 sites located in frost pockets in the "Barrens" of Centre County. Nevertheless, there was never a good crop of white oak acorns produced throughout the first 5 year study period of 1949 to 1953—only spotty, erratic, poor yields on an occasional tree. The only "black freeze," extending over a wide area in Pennsylvania, occurred in late May, 1956. In early May, 1957, another freeze occurred, but it was localized and much of the forest was unaffected. Therefore, over a period of 12 yrs there was only one extensive freeze and only one localized freeze; but a good crop of white oak mast occurred in the unaffected areas in 1957. Good to heavy yields of white oak mast occurred in only 5 of the 12 yrs: 1954, 1957, 1958, 1959, and 1960.

There is a wide difference in opinion as to the temperature which causes frost kill. Zon (1904) stated that temperatures 4-7 degrees above the freezing point caused poor seed years. He did not clearly state whether the freezing point was 32°F or if it was the "killing point." It was learned from observations in 1957 that the tender shoots and catkins in white oaks endured temperatures below 29°F without being seared. White oaks appear to suffer no effects from light frosts (32°-29°F), and the green shoots and catkins tolerate heavy frosts (29°-25°F). But the detrimental effects of such frosts on the immature pollen were not determined. Chandler (1913) in Missouri observed that when peach blooms were subjected to a temperature of 24°F they suffered light to medium frost kill while apple blooms suffered a 75% kill. Frost kill of the pollen varied with the variety: Jonathan apple was more resistant to frost than the Rome Beauty (Lommel and Green 1930). Pollen is perhaps more resistant to frost kill than the anthers or their filaments, for Chandler found that pollen withstood a temperature of —8°C or 17.6°F.

Had our study terminated at the close of 1953, after a period of 5 years, erroneous conclusions would have been reached. Desiccating atmospheric conditions or killing frosts would have been considered of no consequence in oak pollen production. To have speculated at that time on the reasons why the female flowers failed to produce acorns would have resulted in even more erroneous conclusions because, during the years 1949 through 1953, a good acorn crop was not produced.

SUMMARY

Flowering in the white oaks was initiated prior to bud swelling in 1949. Phases of this work were continued through 1960. This investigation was initiated to determine if adverse weather conditions occurring in the period of male flowering were responsible for good or poor acorn production.

The study area, in the northern Ridge and Valley Province in central Pennsylvania, consisted of white oak sites situated along a transect extending across portions of this province and upon the edge of the Allegheny Plateau. The area encompassed a variety of soil types, physiographical aspects, and altitudinal variations.

Observations on catkin development from the time of emergence through ripening and dispersal of the pollen are reported. The chestnut oak, scrub chestnut oak, and the burr oak showed no seasonal variation in time interval of flowering, but in the white oak there were 3 distinct periods of catkin emergence, characteristic of individual trees. These were called flowering waves—early, medium, and late.

The anther walls of the ripened stamens opened or closed according to the relative humidity. This served as a safeguard against washout of pollen by rain. Complete pollen dissemination from a tree required only a few hours in the scrub chestnut oak to about 3 days in the white oak. Periods of prolonged, wet, rainy weather postponed pollen shedding.

Factors detrimental to male flowering and pollen dispersal were dry desiccating winds and killing freezes.

ACKNOWLEDGMENTS

Appreciation is expressed to Drs. Peter W. Fletcher and R. E. McDermott, School of Forestry, and Lorraine Kapitanoff, Librarian, the Pennsylvania State University; to Drs. Daniel L. Leedy, Eugene H. Dustman, and Richard Manville, Bureau of Sports Fisheries and Wildlife (Department of the Interior); and to R. S. Cowan, Botanist, Smithsonian Institution, Washington, D. C. for critical review and comments on the manuscript. We express our sincere gratitude to Dr. Vance D. Sprague, Pasture Research Laboratory, U. S. Department of Agriculture, University Park, Pennsylvania for his cooperation in providing weather data.

REFERENCES

Baker, F. S. 1950. Principles of Silviculture. McGraw-Hill, N. Y. 414 pp.

Baldwin, H. I. 1942. Forest tree seed of the north temperate regions. Chronica Botanica Co., Waltham, Mass. 240 pp.

Boyd, R. L. and L. P. Latimer. 1933. The relation of weather to pollination of the McIntosh apple. Proc. Amer. Soc. Hort. Sci. **30**: 12-16.

Busgen, M. and E. Munch. 1929. The structure and life of forest trees. John Wiley & Sons, N. Y. 436 pp.

Chandler, W. H. 1913. The killing of plant tissue by low temperature. Res. Bul. 8. Ag. Exp. Sta., Univ. of Mo., Columbia. pp. 143-309.

Dorsey, M. J. 1919. Relation of weather to fruitfulness in the plum. Jour. Agr. Res. **17**: 103-126.

Fenneman, N. M. 1938. Physiography of eastern United States. McGraw-Hill Book Company, N. Y., N. Y. 714 pp.

Geiger, R. 1950. The climate near the ground. Harvard Univ. Press, Cambridge, Mass. 482 pp.

Gray, A. 1879. Structural botany. Amer. Book Co., N. Y. 442 pp.

Haynes, B. C. 1947. Techniques of observing the weather. John Wiley & Sons, N. Y. 272 pp.

Lommel, W. E. and Laurenz Greene. 1930. Some effects of late spring frosts upon the viability of apple pollen. Proc. Amer. Soc. Hort. Sci. **27**: 404-405.

Rendle, A. B. 1925. The classification of flowering plants—dicotyledons. Cambridge Univ. Press, London. **2**: 30-34.

Zon, R. G. 1904. Effects of frosts upon forest vegetation. For. Quart. **2**: 14-21.

SEASONAL TRENDS IN CARBON DIOXIDE ABSORPTION, COLD RESISTANCE, AND TRANSPIRATION OF SOME EVERGREENS[1]

JOHNSON PARKER
William B. Greeley Memorial Laboratory, Yale School of Forestry, New Haven, Connecticut

The evidence for absorption of CO_2 by evergreen trees in winter is considered somewhat controversial by some writers. Bourdeau (1959), for example, cited both Freeland (1944) in northern Illinois and Parker (1953a) in southern Germany to the effect that CO_2-absorption by certain evergreens continues well into early winter, but Bourdeau and certain others mentioned later in this paper found no absorption by various conifers during the entire winter in moderately cold climates.

It therefore seemed of interest to study further the amounts of CO_2 absorbed by some widely different species of conifer, first to verify the concept that evergreens can go on absorbing CO_2 well into late autumn and early winter, at least in certain climates, and secondly, to find out whether conifers native to warm climates behave about the same as conifers native to cold climates in respect to amounts of CO_2 absorbed at different times of the year in a single climate.

---

[1] Longleaf pine and Scotch pine seedlings were loaned by F. Mergen; longleaf pine seed was obtained from the Lake City Florida branch of the Southeastern Forest Experiment Sta., U. S. Forest Service.

Besides this, it seemed of interest to examine the possible cause of the winter decline in CO_2-absorption (e.g., Bourdeau 1959), a decline which must be the result of leaf condition and not necessarily of environmental conditions at the time of measuring. If the effect of lowered CO_2-absorption is the result of an increased cold hardiness, then there should be certain relationships shown to changes and amounts of cold hardiness observed. On the other hand, if the effect is the result of stomatal closure, then one would expect certain relationships to the amount of water transpired. Cold hardiness and transpiration rate were therefore also studied in the same species used in the CO_2 studies.

METHODS

Co$_2$-Absorption

Three species were selected for this study: Scotch pine (*Pinus sylvestris* L.), longleaf pine (*P. palustris* Mill.), and Sawara cypress (*Chamaecyparis pisifera* Sieb. & Zucc.). The cypress was selected for the main studies since a specimen of this species was growing only 10 ft distant from the laboratory on its southwestern side and was nearly tree size: 12 ft tall, 4 in. dbh, and about 10 years old. Although an exotic species, it is native to northern Japan and is widely planted with good success in southern New England. Specimens growing in New Haven are sometimes a foot in diameter at breast height.

The system of sampling and measuring CO_2 was essentially that developed by Huber (1950) and further described by Parker (1953a). A celluloid cylinder, three inches in diameter and eight inches long, was placed over the terminal twig of a branch. Branches on the north as well as the south side, five feet above-ground, were sampled. The cylinder was sealed at the apical end of the branch with a circular disc of plastic. A tygon tube, which had been wound once around the inside of the cylinder and had been perforated with a series of holes each two mm. wide, was led out from the closed terminal end of the cylinder into the laboratory. The other end of the cylinder (toward the trunk) was open to the air. A thermometer was inserted and held in the cylinder with Scotch tape parallel to the long axis and one cm away from the celluloid surface. Its bulb was shielded from the sun with aluminum foil.

Air was run over the leaves in the cylinder and into the laboratory via the tube at a rate of one liter per minute. After 10 minutes of passing air over the plant material, the cylinder was removed and air was sampled from the atmosphere four feet from the tree for comparison; after three to five minutes, air from the plant was again sampled. Sampling began about 9:15 A.M. and continued until about 4:30 P.M. on sampling days. Sampling days are indicated in the results by the data plotted (Figures 1 and 2).

All air drawn into the laboratory was passed through a glass column with 200 cc of oven-dry $CaCl_2$ to remove water vapor, then into a Fisher diaphragm pump, and finally into a Beckman Model 15 infra-red gas analyzer. Readings were recorded continuously on an Esterline-Angus chart recorder.

Three-year-old seedlings of Scotch pine and longleaf pine in clay pots were selected which had been grown from seed in the greenhouse. Eight individuals of each species were put out-of-doors on August 30, 1959, and eight kept in the greenhouse. Seedlings numbered 1 to 4 for each species and treatment were used for the cold resistance studies described below. For the CO_2-absorption measurements, one individual of the seedlings numbered 5 to 8 was sampled on a particular day for each species. Field (out-of-doors) seedlings were kept buried up to their root collars in sawdust in a nursery bed adjacent to the laboratory and were unearthed for sampling and brought to the south side of the laboratory for CO_2 measurements. Greenhouse seedlings were kept in pots on gravel, and unlike field plants, watered each day. These were likewise brought to the south side of the laboratory for measurements. The cylinder was placed over a lateral branch of a Scotch pine seedling or over a needle cluster of longleaf pine. Leaves sampled were tied with a string so that the same leaves would be used subsequently.

Normally the cypress was sampled for 10 minutes in the early morning, then one of the longleaf pines, then a Scotch pine. This sequence was repeated at 10:30 A.M., 1:30, and 3:00 P.M. Rates of CO_2-absorption (Fig. 1 for cypress, 2 for pines) were maxima for the day: the difference between the recorded meter reading for outside air and air drawn over the leaves in per cent of CO_2 in the atmosphere.

Hardiness

Studies of this condition were carried out mainly as before (Parker 1957a, 1959). Three-inch

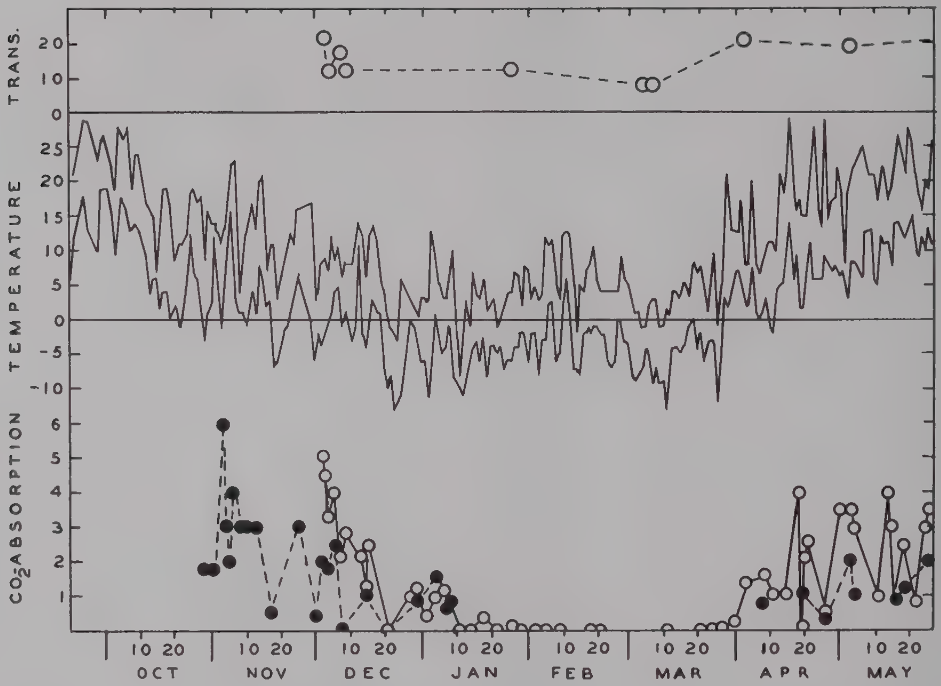

FIG. 1. "Trans" = transpiration from cypress in 10ths of mg / g freshweight leaf (with twig wood). "Temperature" = maximum and minimum temperatures daily in °C. "CO_2-Absorption" is given for the south side of the cypress (open circles) and north side (blacked-in circles) in terms of the difference between per cent of CO_2 in the air near the tree and air after passing over leaves, × 1000, for a twig weighing 16 g fresh weight.

long cuttings were made from the cypress tree at 4:00 P.M. on a sampling day (shown in Fig. 3) and placed in Dewar flasks. Starting at 8:00 A.M., leaves were cooled at 5°C change per hour in the low temperature apparatus after being held at 0°C overnight (16 hours). Leaves of white pine (*Pinus strobus* L.), hemlock (*Tsuga canadensis* [L.] Carr.), yew (*Taxus baccata* L.), and *Rhododendron* spp. were similarly sampled from the Marsh gardens adjacent to the laboratory for sake of comparison to the cypress. The same tree or shrub was always sampled for each species. After reaching a certain low temperature, they were warmed at about 8°C rise per hour to room temperature (23°C). Viability was determined by placing leaves in a "desiccator" over distilled water for at least three weeks. If the leaf color change (to dull green or brownish) occurred within three weeks, they were considered dead. If still green and normal appearing at the end of this period, they were considered alive. This criterion has been verified by other methods, such as the tetrazolium test (Parker 1953b), although the best length of time for keeping the leaves in the humidity chamber is a difficult thing to establish.

Cold resistance studies were also made on four Scotch pines and four longleaf pines from the greenhouse, and on four of each species kept in the field numbered 1 through 4. Each individual seedling was sampled and labelled separately so that variations in individuals could be followed and compared. Sampling times are shown in Figure 4.

Maximum and minimum temperatures were read each morning at 9:00 A.M. on a Six-type thermometer kept in a standard Weather Bureau shelter 50 feet from the cypress tree and 100 feet from the pines on the south side of the laboratory.

Transpiration

Cuttings about three inches long were made from the Sawara cypress and brought into the laboratory within two minutes where they were weighed every minute for eight minutes on a balance sensitive to tenths of a milligram at a constant temperature of 25°C and a relative humidity of 44 ± 5 per cent. This is somewhat similar to the

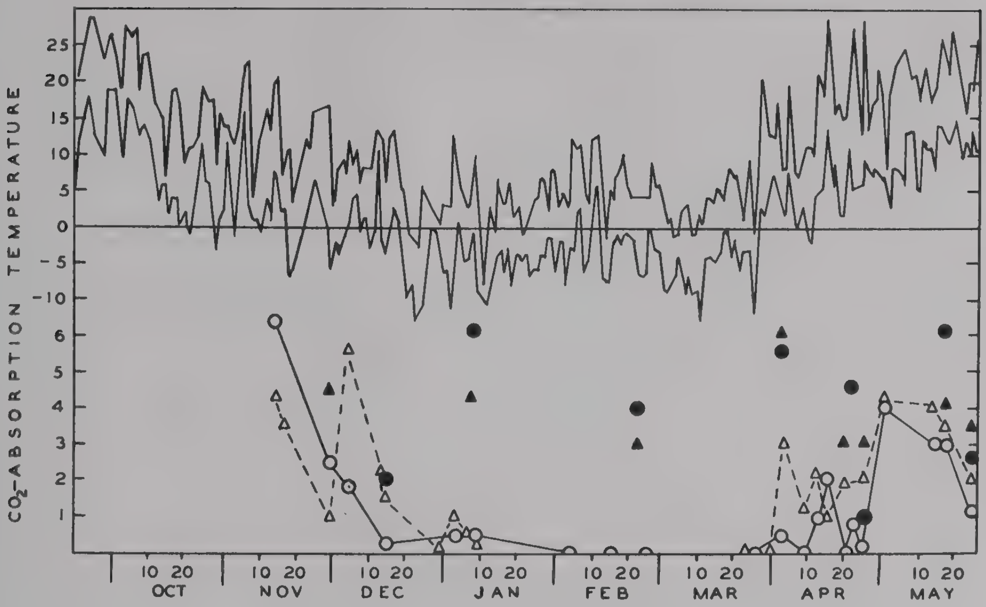

FIG. 2. "Temperature" = maximum and minimum temperatures daily in °C. "CO_2-Absorption" is given as in Figure 1, but for 41 g of leaf fresh weight for longleaf pine and 11 g of leaf for Scotch pine (without twig wood). Data are given for only one of the Scotch pines and one of the longleaf pines. Triangles = longleaf pine; circles = Scotch pine. Darkened circles and triangles = greenhouse pines; open circles and triangles = field pines.

procedure used previously (Parker 1957b) to estimate transpiration from tree leaves, except that cut ends were not coated with vaseline and weighings were carried out in a constant temperature room. Leaves of Scotch pine seedlings were similarly cut from twigs and single fascicles hung on the balance hook for measurement of weight loss. Single longleaf pine leaves were cut from the seedlings, bent in the middle, and hung on the balance hook at the point of bending, then weighed every minute for eight minutes. The cypress was sampled approximately each month and the pines about every other month.

RESULTS

Sawara Cypress

CO_2-Absorption Rates.—Rates were as high in November as at any time during the period of testing (November to June). On November 10th when maximal readings were recorded even on the north side (Fig. 1) the leaves had almost entirely fallen from adjacent maples (*Acer platanoides* L.) and red oaks (*Quercus rubra* L.), while leaves of beech (*Fagus grandifolia* Ehr.) had turned a yellowish brown. Even after a severe frost in mid-November, CO_2-absorption continued at a high rate. This was especially true on the south side of the cypress. By late December, rates were reduced to about a third of their former level (Fig. 1). The more severe cold in late December seemed related to the subsequent decline in rates of absorption in early January. This decline was apparently not the result of lower operating temperatures since there were occasional periods of warm weather. By early February, rates were unmeasureable on days when the temperature was above freezing.

Diurnal trends in December on the south side usually developed a plateau-like curve (graph not shown) when absorption was plotted over time of day: it rose to a maximum by 9:15 A.M. and maintained this level until nearly sundown. This was particularly true on cloudy days when there was little variation in light intensity. Rates on sunny days were often even a little lower than on cloudy days. On one very dark, cloudy day in early January, when it was snowing hard and the air temperature was 0°C, there was still a steady amount of CO_2-absorption throughout the entire day. In spring, on the other hand, there was frequently a decline in CO_2-absorption to about a half the 9:15 rate by 11:00 A.M. on the south side, then a slight recovery by 2 P.M. The north side came up sooner in the morning because of the sun striking the leaves sooner, declined by noon to

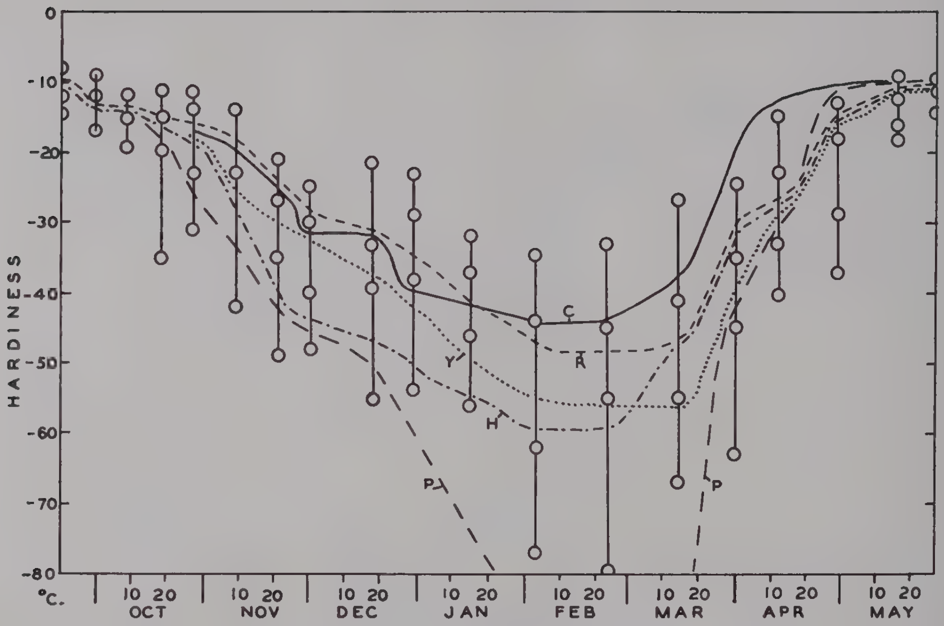

Fig. 3. Cold hardiness in °C for Rhododendron (R), Sawara cypress (C), white pine (P), hemlock (H), and yew (Y). Each vertical line connecting a series of circles includes temperatures to which leaves were cooled on a particular day. Lines (dotted, dashed, etc.) are drawn as closely as possible to the estimated point at which 50% killing of leaves was obtained for each determination on any date. If one temperature killed the leaves and the next did not, the line was drawn between these points. New leaves in spring not represented.

about half the morning level, and remained steady until sundown.

All through February, absorption was nil. On sunny days in this month, the cylinder temperature sometimes rose as high as 20°C. Under these conditions a definite respiratory activity (CO_2-release) was measureable from the leaves. March was exceptionally cold as compared to past years, but when temperatures rose starting March 28th, some CO_2-absorption was again recorded on April 1st (Fig. 1). Absorption then rose to higher levels by late April. Since leaves of the adjacent red oak were barely emerging from the buds by May 1st, the cypress possesses an obvious seasonal advantage.

Hardiness.—Seasonal trends in hardiness in the cypress are compared to the other species in Figure 3. Cypress generally followed the same seasonal trends as the other evergreens, but it did not appear to be quite as hardy in winter as the others and dehardened somewhat sooner than the others in spring.

The relationship between hardiness and rates of CO_2-absorption appears to be roughly related in cypress. Yet when hardiness was nearly fully developed in early January, CO_2-absorption could still be recorded, although this absorption later declined to zero. In spring dehardening began by mid March, but a positive rate of CO_2-absorption was not measureable until the end of March. It thus appears that there is only a rough, but not exact, relationship between hardiness and CO_2-absorption in this species.

Transpiration.—Although CO_2-absorption ceased by the end of January, transpiration continued to occur throughout the winter from the cypress (Fig. 1). Rates of weight loss were between 12 and 24 tenths of a mg per g fresh weight in early December at noon. This rate declined to 11 in late January and to 7 by early March. By April 4th, however, the rate increased to 20 and remained at about this level through May and early June. This suggests that the stomatal opening and recovery of CO_2-absorption in spring are not exactly related, but data are probably not precise enough to draw very positive conclusions on this. Leaf water content, in the meantime, did not change appreciably with the season.

Pines

CO_2-Absorption Rates.—In longleaf pine and Scotch pine kept out-of-doors, rates of CO_2-ab-

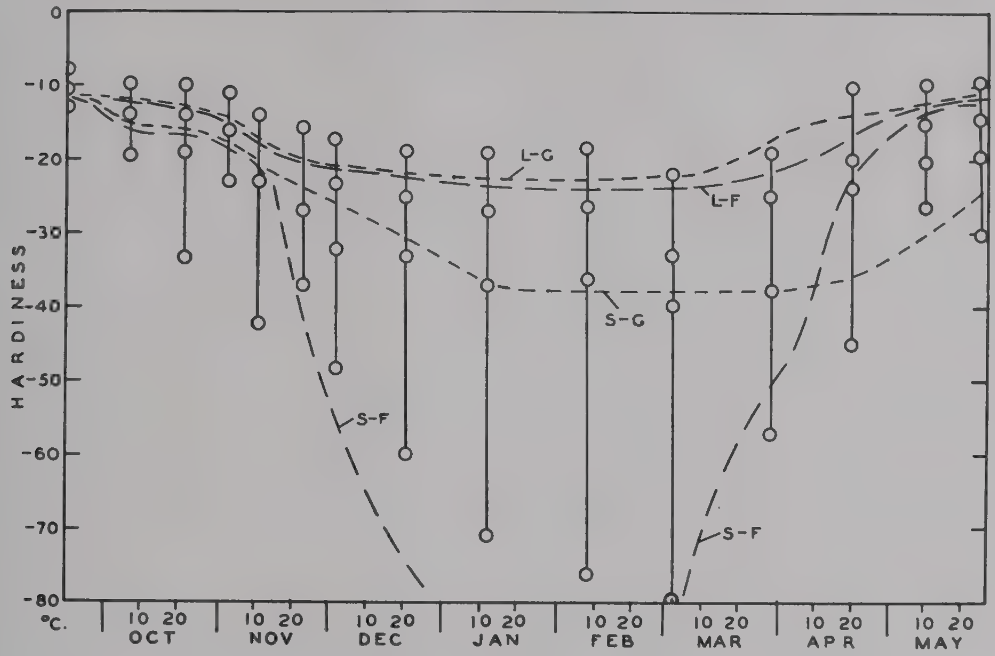

FIG. 4. Cold hardiness in °C for greenhouse longleaf pine (L-G), field longleaf pine (L-F), greenhouse Scotch pine (S-G), and field Scotch pine (S-F). Lines are drawn as in Figure 3 to show approximate hardiness at 50% killing.

sorption were similar to those of cypress (cf. Figs. 1 and 2). This is remarkable considering the diversity in morphology, origin, and hardiness of these three species of conifers. Some absorption was recorded even in January in longleaf pine (Fig. 2), an observation that seems surprising in view of its origin in northern Florida.

In the meantime, seedlings of longleaf pine and Scotch pine brought out-of-doors from the greenhouse for CO_2-measurements were able to absorb relatively large amounts of CO_2 at various times of winter (Fig. 2). This shows that operating temperatures were not the cause of the low rates in the field pines. In spring, rates of CO_2-absorption were often difficult to compare between species, since rates came up rapidly in the morning and declined sharply by noon, some plants declining sooner than others.

Differences among individual Scotch pines were not great, but longleaf pines in early spring varied considerably from one another, possibly related to the slight winter damage that partially browned the leaves, especially towards the tips.

Hardiness.—Trends for the two pine species and for the two treatments (greenhouse and field) are shown in Figure 4. The field Scotch pine became far hardier than the greenhouse Scotch pine, but the greenhouse Scotch pine became somewhat more cold hardy in winter than in autumn. This seasonal increase in hardiness in greenhouse Scotch pines is apparently the result of naturally shorter day-lengths, since temperature changes in the greenhouse were not involved and since parallel experiments with white pine (*Pinus strobus* L.), grown under various day-lengths in the greenhouse by F. Mergen and tested by the writer, showed that hardiness was brought on sooner by artificially-shortened days and was delayed by artificially-lengthened days.

There was a marked similarity in hardiness trends in the two treatments (field and greenhouse) for longleaf pine. This suggests that hardiness in both greenhouse and field plants of this species is developed endogenously or under the influence of day-length and that low temperatures in the field do not do much to improve hardiness, at least in this variety of longleaf pine. Field longleaf pine did not even develop the hardiness of Scotch pine in the greenhouse. In the spring, there was, however, a divergence of trends in the two treatments for longleaf pine: the greenhouse pine dehardened sooner than the field pine and the former began growth sooner. In Scotch pine the reverse was true: the field seedlings dehardened sooner than the greenhouse seedlings. The time of dehardening of either of the pine species was related to the resumption of shoot growth as noted previously (Parker 1959).

The increase in hardiness of Scotch pine in the field in autumn and the decrease in spring appear to be related in time to the CO_2-absorption trends, at least in a rough way, but greenhouse Scotch pine was hardier than field longleaf pine, yet the former absorbed far more CO_2 than the latter. In longleaf pine, CO_2-absorption was entirely unrelated to hardiness, since field longleaf pine possessed about the same hardiness as the greenhouse longleaf pine, while CO_2-absorption rates were high in the greenhouse pine and entirely nil in the field pine in February (Figure 2).

Transpiration and Water Content.—It might be suspected that the lowered rate of CO_2-absorption in the field pines in winter could be the result of leaf dehydration and thus of stomatal closure. Actually, however, a test of leaf moisture content in three seedlings of each species for each of the two treatments in late February showed that water content was about the same as in the growing season. The greenhouse longleaf pine contained even somewhat less water on the average per dry weight of leaf than the field pines and there was no significant difference in water content between the two treatments for Scotch pine.

In either of the two species of pines, transpiration was roughly related to CO_2-absorption rate (not shown in graphs). For example, the greenhouse transpiration of Scotch pine on February 29th at noon was 10 times as great as that in the field, and in longleaf pine 23 times as great. Transpiration was, in fact, barely measureable in the field plants. These results compare favorably with the rates of CO_2-absorption which were nil in the field at this time, but high in the greenhouse in either species. Yet this relationship between transpiration and CO_2-absorption was not always perfect. For example, in spring, although one of the longleaf pines began to transpire more rapidly than in winter, recovery of the CO_2-absorption rate to measureable quantities did not occur for several more days, later on in April.

DISCUSSION

It has been apparent for many years that curtailment of photosynthesis by cold weather depends to a great extent on the kind of environment to which the plant is subjected. Near the tree-line in the Austrian alps there is usually a definite prolonged rest period in *Pinus cembra* during which there is no measureable gas exchange at all (Cartellieri 1935). A single frost in autumn was not enough to begin the condition of cessation of gas exchange, but according to Cartellieri, a second hard frost did bring it on. This situation was verified by Tranquillini (1952, 1955, 1957) and by Pisek and Winkler (1958) who made many of their measurements at the tree-line (1840 m) near Innsbruck. Pisek and Winkler suggested that the limitation of the forest at the tree-line may well be greatly influenced by this phenomenon.

Tranquillini (1957) found that after a strong frost in early November at this tree-line habitat there was a reduction of photosynthesis to one tenth of the summer rate in *Pinus cembra*, then there followed a series of exceptionally cold days (minima —10 to —15°C) at which time there was nearly a complete "paralysis" of the photosynthetic apparatus during which time no CO_2-absorption could be measured. This situation persisted all the way from November to May. Their results in the high mountains therefore appear to resemble those of Bourdeau (1959) in lower New York state for several species of conifers.

On the other hand, it has been known for many years that some plants can carry on photosynthesis during the colder months in fairly cold climates, and it has been known since the time of Boussingault (1855, cited by Ehlers 1915) that leaves can evolve oxygen at temperatures near the freezing point. Some plants are capable of carrying on photosynthesis even at temperatures below 0°C (Kreusler 1888, Jumelle 1891, Mathäi 1914, cited by Zacharowa 1929).

As early as 1915 Ehlers pointed out that carbohydrate could be accumulated in leaves of conifers in winter in the climate of Ohio. He believed that winter carbohydrate production depended to a large extent on weather conditions preceding the determinations. Henrici (1921) likewise pointed out that various kinds of evergreen plants as well as broad-leaved shrubs can carry on photosynthesis during the winter months in the cooler parts of South Africa. Guttenberg's publications (1927, 1928) further supported the idea that there was some carbohydrate manufactured in winter, although he considered it so small that the slight outward translocation in winter prevented any accumulation in most winter months.

According to Zacharowa (1929) some species are more capable of continuing photosynthesis into the winter than others. Working near Moscow, Russia, Zacharowa found that *Picea excelsa* could go on absorbing CO_2 several weeks more than could *Pinus sylvestris*. This seemed to be associated with changes in chloroplast condition. Spruce also resumed activity sooner in spring than pine.

Although Ivanov and Kossovitsch (1929) concluded that there was no CO_2-absorption in *Pinus sylvestris* in winter near Petersburg in Russia, Ivanov and Orlova (1931) later found that there was a small, but definite amount absorbed in every month of winter (graph republished by Pisek and Winkler, 1958). This final conclusion agrees with the findings of Zeller (1951) near Stuttgart who showed that although photosynthesis was much reduced in winter in *Picea excelsa*, there was a positive (net) CO_2-absorption in December, January, a trace in February, then more in March. She concluded that the "winter-rest" was not absolute although it was more pronounced in spruce than in winter annuals such as the hardy field spinach. These conclusions appear fully supported by the findings of Freeland (1944) who showed that in northern Illinois conifers can go on absorbing CO_2 nearly all through the winter. Using seedlings of *Picea mariana, Pinus sylvestris,* and *Pinus nigra,* positive CO_2-absorption continued into January and reappeared again in March. Results collected by Huber, Hey, and the writer near Munich (Parker 1953a) clearly showed positive rates of CO_2-absorption in *Picea excelsa* into early December, at which time the work was discontinued. Pisek and Winkler (1958) working at the Botanical Gardens in Innsbruck (600 m) found a definite net photosynthesis in December (one third of the summer rate) and still a positive rate in January. After a period of no activity at all during a cold February, a level was reached in March about equal to the December rate. This somewhat resembles data recorded in the present paper. McGregor (1958) likewise found that there was a decline in photosynthesis in *Pinus taeda* and *P. strobus* in winter in North Carolina, and that although respiration exceeded absolute photosynthesis in January and February, there were still positive net rates of CO_2-absorption in November and March (measured at 25°C and 4,000 ft-candles). Saeki and Nomoto (1958) found net photosynthesis throughout the winter in two evergreens of Japan.

Even when no CO_2 is being absorbed at all in winter, it is possible that light energy is being stored through the chloroplast system (which according to our microscopic observations in several evergreen species only undergoes a clumping, while others do not even do this) and through adenosine phosphate compounds (Arnon et al. 1958). Besides this, carbonate might be derived in small part from xylary water for photosynthesis and thus atmospheric absorption might be unmeasureable while photosynthesis proceeded. For these reasons we have avoided the word "photosynthesis" in the methods and results of this paper. Even the branches of deciduous trees which contain some chlorophyll in the cortex and inner bark might be able to manufacture sugar and amino acids in winter.

In view of all this work it is neither surprising to find some CO_2-absorption occurring in winter nor to find it entirely lacking in certain climates. Much seems to depend on the severity of the cold weather and this can, of course, vary widely from climate to climate.

SUMMARY

1. Seedlings of Scotch pine (*Pinus sylvestris* L.), seedlings of longleaf pine (*P. palustris* Mill.), and a tree of Sawara cypress (*Chamaecyparis pisifera* (Sieb. & Zucc.) growing out-of-doors at New Haven, Connecticut continued to absorb amounts of CO_2 in early November which were among the highest rates measureable in the period from November to June, even though adjacent deciduous trees had largely lost their leaves in early November. Rates declined to about one third of the November levels by late December and to about half of the average December rates by early January. Although none was absorbed in February or during an exceptionally cold March, positive (net) absorption occurred on April 1st about 3 days after the beginning of a definite warm period and about 4 weeks before the opening of leaves of most native deciduous trees. The rate then gradually increased in late April and May.

2. Very little difference in CO_2-absorption rates among the three coniferous species was indicated by the seasonal trends: all declined in autumn and winter and recovered in spring at about the same time. In longleaf pine in spring there was some individual variation in recovery of CO_2-absorption.

3. Although CO_2-absorption levels and hardiness levels were to some extent related seasonally in cypress and Scotch pine, hardiness and CO_2-absorption were apparently unrelated in longleaf pine. By mid-winter, greenhouse longleaf pine was nearly as hardy as that from the field, yet greenhouse pines continued at a high rate of CO_2-absorption throughout the winter, while field longleaf pine absorbed only slight amounts of CO_2 in January and ceased in February. Greenhouse Scotch pine became even hardier than field longleaf pine in early winter, but this Scotch pine had a much greater CO_2-absorption rate than field longleaf pine in winter.

4. Seasonal changes in CO_2-absorption rates were roughly related to transpiration in all three species. But exact relationships were lacking in several cases (transpiration data for pines not presented).

5. Transpirational decline in winter was not the result of a lowered leaf water content, since leaf water contents remained about the same as in the growing season.

6. Maximum hardiness of longleaf pine in the field was approximately —24°C, Sawara cypress —43, *Rhododendron* spp. —48, yew (*Taxus baccata* L.) —56, hemlock (*Tsuga canadensis* [L.] Carr.) —58, Scotch pine about —80 and white pine (*Pinus strobus* L.) lower than —77°C. In both Scotch pine and longleaf pine for either treatment there was no significant difference among different individuals in hardiness.

7. Greenhouse Scotch pine and longleaf pine increased in hardiness in autumn apparently because of day-length shortening, judging partly by parallel experiments with white pine. Longleaf pine, unlike Scotch pine, apparently did not require a cold period to resume growth and deharden in April.

REFERENCES

Arnon, D. I., F. R. Whatley, and M. B. Allen. 1958. Assimilatory power in photosynthesis. Science **127**; 1026-1034.

Bourdeau, P. F. 1959. Seasonal variations of the photosynthetic efficiency of evergreen conifers. Ecology **40**: 63-67.

Ehlers, J. H. 1915. The temperature of leaves of *Pinus* in winter. Amer. Jour. Bot. **2**: 32-70.

Cartellieri, E. 1935. Jahresgang von osmotischem Wert, Transpiration und Assimilation einiger Ericaceen der alpinen Zwergstrauchheide und von *Pinus cembra*. Jahrb. f. wiss. Bot. **82**: 460-506.

Freeland, R. O. 1944. Apparent photosynthesis in some conifers during the winter. Plant Physiol. **19**: 179-185.

Henrici, M. 1921. Zweigipfelige Assimilationskurven. Mit spezieller Berücksichtigung der Photosynthese von alpinen Phanerogamen, Schattenpflanzen und Flechten. Verh. naturforsch. Ges. Basel **32**: 107. [Cited by Pisek and Winkler, 1958].

Guttenberg, H. von. 1927. Studien über den Verhalten des Immergrünenlaubblattes der Mediterranflora zu verschiedenen Jahreszeiten. Planta **4**: 726-779.

———. 1928. F. A. Preisings Untersuchungen über den Kohlenhydratstoffwechsel immergrüner Blätter im Laufe eines Jahres. Planta **6**: 801-808.

Huber, B. 1950. Registrierung des CO_2-Gefälles und Berechnung des CO_2-Stromes über Pflanzengesellschaften mittels Ultrarot Absorptionsschreiber. Ber. d. deutsch. Bot. Ges. **63**: 53-64.

Ivanov, L. A. and N. L. Kossovitsch. 1929. Über die Arbeit des Assimilationsapparates verschiedener Baumarten. I. Die Kiefer (*Pinus sylvestris*). Planta **8**: 427-464.

——— **and I. M. Orlova.** 1931. Zur Frage über die Winter-Assimilation von Kohlensäure unserer Nadelhölzer. Zeit. Russ. Bot. Ges. **16**: 139 [Cited by Pisek and Winkler, 1958].

Kramer, P. J. and T. T. Kozlowski. 1960. Physiology of Trees. McGraw-Hill, New York.

McGregor, W. H. D. 1958. Seasonal changes in the rates of photosynthesis and respiration of loblolly pine and white pine. Ph.D. dissertation, Duke Univ., Durham, N. C. [Cited by Kramer and Kozlowski, 1960: 73].

Parker, J. 1953a. Photosynthesis of *Picea excelsa* in winter. Ecology **34**: 605-609.

———. 1953b. Criteria of life: some methods of measuring viability. Amer. Scientist **41**: 614-618.

———. 1957a. Seasonal changes in some chemical and physical properties of living cells of *Pinus ponderosa* and their relation to freezing resistance. Protoplasma **48**: 147-163.

———. 1957b. The cut-leaf method and estimations of diurnal trends in transpiration from different heights and sides of an oak and a pine. Bot. Gaz. **119**: 93-101.

———. 1959. Seasonal variations in sugars of conifers with some observations on cold resistance. For. Sci. **5**: 56-63.

Pisek, A. and E. Winkler. 1958. Assimilationsvermögen und Respiration der Fichte (*Picea excelsa* Link) in verschiedener Hohenlage und der Zirbe (*Pinus cembra* L.) an der alpinen Waldgrenze. Planta **51**: 518-543.

Saeki, T. and N. Nomoto. 1958. On the seasonal change of photosynthetic activity of some deciduous and evergreen broadleaf trees. Bot. Mag. Tokyo **71**: 235-241 [Cited by Kramer and Kozlowski 1960: 74].

Tranquillini, W. 1952. Der Ultrarot-Absorptionsschreiber im Dienste ökologischer Messungen des pflanzlichen CO_2-Umsatzes. Ber. d. deutsch. bot. Ges. **65**: 102-112.

———. 1955. Die Bedeutung des Lichtes und der Temperatur für die Kohlensäureassimilation von *Pinus cembra*-Jungwuchs an einem hoch alpinen Standort. Planta **46**: 154-178.

———. 1957. Standortsklima, Wasserbilanz und CO_2-Gaswechsel junger Zirben (*Pinus cembra* L.) an der alpinen Waldgrenze. Planta **49**: 612-661.

Zacharowa, T. M. 1929. Über den Gastoffwechsel der Nadelholzpflanzen im Winter. Planta **8**: 68-83.

Zeller, O. 1951. Über Assimilation und Atmung der Pflanzen im Winter bei tiefen Temperaturen. Planta **39**: 500-526.

FACULTATIVE HETEROTROPHY IN CERTAIN SOIL ALGAE FROM THE ECOLOGICAL VIEWPOINT

Bruce C. Parker
Department of Botany, University of Texas, Austin, Texas[1]

Introduction

Heterotrophism in algae has been discussed by Petersen (1935), who reviewed the early literature including especially the studies of Bristol-Roach (1926, *et seq.*). He also noted that, of the 3 major groups of algae found commonly in soils (Chlorophyceae, Cyanophyceae, and Bacillariophyceae), only the Bacillariophyceae then remained in question as possessing at least some facultatively heterotrophic species. More recently, facultative heterotrophy has been demonstrated *in vitro* for some algae belonging to each of these major groups (Myers 1951, Lewin 1953, Fogg 1953, Saunders 1957, Palmer 1959, Von Ernst and O. Pringsheim 1959, Lewin and Lewin 1960, Belcher and Miller 1960, Parker, Bold and Deason, in press). Such algae have been obtained mostly from fresh-water, marine and soil habitats.

The routine method for detection of facultative heterotrophy in algae is the inoculation of a relatively small quantity of cells from a pure culture into a basal medium enriched with a single carbon source. Cultures are stored in total darkness under standard conditions for a period adequate to produce visible detectable growth. A negative result indicates that the alga is unable to grow significantly on the particular substrate and under the experimental conditions.

Glucose is the most common substrate for routine investigations and generally has given the greatest success. Concentrations customarily range from 0.1-1.0%, which is much higher than that found normally in the natural habitat of the organisms. For this reason, the demonstration of facultative heterotrophy in algae by routine methods is, at best, only presumptive evidence for facultative heterotrophy in nature. Attempts to demonstrate facultative heterotrophy in soil, most of which have been reviewed by Petersen (1935) and later discussed by Fritsch (1936) and John (1942), have been either unsuccessful or of doubtful validity. Since treatment of the subject by these investigators, little attention has been focused on experiments of this nature, and the subject has remained unresolved.

This investigation was undertaken to determine whether certain algae from the Univ. of Texas campus soil could grow on carbon or energy substrates derived from the original soil. It involved 3 phases, as follows: (1) testing algal isolates for ability to grow in darkness in a defined glucose-salts medium; (2) testing a selected facultative heterotroph from phase (1) in both pure and monaxenic (i.e., two-membered), soil-water cultures in darkness; and (3) testing the same selected alga in pure, ashed and unashed, soil-extract cultures at sub-optimal light intensities to ascertain if organic compounds in the soil extract could supplement the energy for growth obtained from light.

Routine Examination for Facultative Heterotrophy in Defined Glucose-Salts Medium

Results of the preliminary tests for facultative heterotrophy are in Table I. In all cases the basal medium employed was B solution.[2] Erlenmeyer flasks containing 50 ml of B solution were autoclaved. After cooling, 0.5 ml of a sterile 20% glucose solution were added aseptically to each flask. Triplicate flasks of this B-glucose solution were inoculated with pure cultures of each algal isolate from cultures actively growing on B agar (B solution + 1.5% agar) slants. The experimental flasks were stored in total darkness for 3 wks at 23°C. Cultures were then examined macroscopically and microscopically for growth and measurements of pH and tests for contamination were made.

---

[1] Portion of a dissertation submitted to the Graduate School, University of Texas, 1960. The investigations were supported by a research grant to Professor Harold C. Bold from the National Science Foundation (NSF G-6373). The writer wishes to acknowledge the kind assistance of Professors Bold and Jack Myers.

[2] The macronutrient solution has been described by Bold (1949); to each liter of this one adds 1 ml of each of the following micronutrient stock solutions:

EDTA Stock—50 g. EDTA plus 31 g. KOH/L.
H-Boron Stock—11.42 g. H_3BO_3/L.
H-Fe Stock—4.98 g. $FESO_4 \cdot 7H_2O$/L. acidified* H_2O

H-H_5 Stock—$ZnSO_4 \cdot 7H_2O$	8.82 g.
$MnCl_2 \cdot 4H_2O$	1.44 g.
MoO3	0.71 g.
$CuSO_4 \cdot 5H_2O$	1.57 g.
$Co(NO_3)_2 \cdot 6H_2O$	0.49 g.

all/L. acidified* H_2O

*acidified H_2O = 999 ml distilled H_2O + 1.0 ml conc. H_2SO_4.

TABLE I. Facultative heterotrophy of some soil-algal isolates in B-glucose solution. Data represent averages of triplicate cultures except in the case of pH readings where averages of duplicate determinations occur

Algae	Relative Growth	Final pH	Microscopic observations
Bracteacoccus A-20	++	5.3	cells light orange; growth diffuse.
Bracteacoccus 9	++	5.9	cells light green; growth diffuse.
Bracteacoccus 1b	++	6.0	cells pale yellow; growth diffuse.
Bracteacoccus A-1	+++	6.6	cells green, growth diffuse.
Bracteacoccus 8b	++	5.0	cells light orange; growth diffuse.
Bracteacoccus 3	++	6.2	cells green; not diffuse, clumped on bottom.
Neochloris 4	+	5.6	cells light green; growth diffuse.
Neochloris 12	+	5.6	cells light green; growth diffuse.
Chlamydomonas 10	—	5.6	faded after 2 wk.
Chlamydomonas 2b	—	5.6	faded after 2 wk.
Phormidium 14	—	—	inoculum bleached; medium toxic.
Hantzschia 11	—	—	no growth in this medium.

Results

The data from these studies are in Table I. All eight chlorococcalean algae (the first 8 listed) from the Texas soil sample grew heterotrophically in B-glucose solution while the algae belonging to other taxa did not grow visibly under the experimental conditions. A reduction in pH occurred in several cultures, especially those of *Bracteacoccus* A-20 and *Bracteacoccus* 8b. Table I includes also some notable differences in the cellular morphology of the species.

Test for Facultative Heterotrophy of *Bracteacoccus* A-20 in Axenic (Pure) and Monaxenic (Two-membered) Soil-Water Cultures

Bracteacoccus A-20 was studied further because it (1) was facultatively heterotrophic in defined glucose-salts medium, (2) utilized a greater spectrum of organic compounds than the other isolates, and (3) was stimulated in growth when cultivated in illuminated soil-water cultures in association with a heterotrophic bacterium. The causal mechanism of the bacterial stimulation was due to the ability of the bacterium to decompose complex nitrogenous substrates in the Texas soil-water medium and to release a portion of the nitrogen in simplified form which was utilized for algal growth (Parker and Bold, in press).

The Texas soil-water flasks (TSWF) were prepared as follows: 15 grams of soil from the original sample site were placed in each of 18 flasks; 60 ml of distilled water were added to each and the flasks were sterilized 15-20 min at 121°C. After cooling, 6 TSWF received a small inoculum from a pure culture of *Bracteacoccus* A-20; 6 more were inoculated with a pure culture of the bacterium (B-6); and the remaining 6 were inoculated uniformly with both organisms. All flasks were stored in darkness. At the time of the initial inoculations, comparable inocula of algal cells were dispensed into 3 flasks of B solution and plated immediately in B agar for initial cell counts. At 3 month intervals one flask from each set was removed from darkness and examined microscopically for algal and bacterial cells. This was repeated 3 times until three flasks of each original set remained in darkness. These remaining cultures were then removed from darkness after 14 months; immediate tests for purity and cell counts by dilution-plating were initiated.

Cell counts and averages for *Bracteacoccus* A-20 are in Table II. No significant increase in cell numbers resulted in the TSWF containing pure cultures of *Bracteacoccus*. However, when associated with the heterotrophic bacterium (B-6) there was a 16-fold increase in algal cells over the original inoculum and axenic (pure) cultures.

TABLE II. Facultative heterotrophy of *Bracteacoccus* A-20 in pure (axenic) and monaxenic soil-water cultures with bacterium B-6

Conditions	No. cells/ml.	Avg. no. cells/ml.
Bracteacoccus in pure TSWF cultures at zero time	3.0×10^3 3.0×10^3 4.0×10^3	3.3×10^3
Bracteacoccus in pure TSWF cultures after 14 mo. in darkness	3.5×10^3 1.0×10^3 3.0×10^3	2.5×10^3
Bracteacoccus + B-6 bacterium in TSWF cultures after 14 mo. in darkness	42.5×10^3 59.5×10^3 52.0×10^3	51.3×10^3

Photoheterotrophism of Pure Cultures of *Bracteacoccus* A-20 in Extracts of Texas Soil

The 14-month dark-cultivation experiment was not repeated; however, reports of several investigators, notably Bristol-Roach (1927, 1928), Pruess et al. (1954), and Killam and Myers (1956), suggested an alternative approach to the confirmation of the hypothesis that *Bracteacoccus* A-20 was capable of assimilating organic substrates from the unenriched soil of the alga's natural habitat. Two experiments are cited.

Experiment 1

One liter of soil extract was prepared as follows: approximately one kilogram of Texas soil and one liter of distilled water were combined in a 2-liter flask and autoclaved at 100°C for 15 min. The hot contents were filtered and the yellow filtrate was collected. It was restored to one liter and divided into 2 equal volumes. One 500 ml aliquot was refrigerated; the second was dried at

105°C until a slurry of about 20 ml remained. This was transferred to a crucible, with water from several rinsings of the original container. The crucible contents were evaporated, then ashed at 800-1000°C for about 2 hr. When cool, the ashed soil extract was removed again with successive rinsings and stirrings, and made up to 500 ml with distilled water.

To each 500 ml portion (one ashed and the other not), 167 ml of B solution was added to make the following 2 media: (1) unashed Texas soil extract with 25% B solution (unashed TSE-25% B) and (2) ashed Texas soil extract with 25% B solution (ashed TSE-25% B). The B solution was added to replace ammoniacal nitrogen and certain other inorganic constituents which might have been lost or decreased by ashing. Both ashed and unashed media had a pH of 7.5 Each medium was divided into 50 ml portions in flasks and autoclaved.

Six flasks of each basal medium received 2 drops of vitamin mix[3] aseptically. Three vitamin-enriched and 3 non-vitamin-enriched flasks containing the ashed TSE-25% B received aseptically 0.50 ml of a 20% glucose solution. Triplicate sets of media were inoculated with a single drop of a uniform suspension of *Bracteacoccus* A-20 cells from an actively growing B-solution culture. Flasks were placed in a dim-light chamber with relatively uniform light of 10 ft-c intensity. An identical triplicate set of inoculated flasks was placed in a bright-light culture chamber at an intensity of about 300 ft-c. In both chambers the illumination was regulated on a 12 hr diurnal cycle at 23°C. After a 2 wk cultivation, all flasks were removed. Tests for purity in nutrient broth, measurements of pH, macroscopic and microscopic observations, and cell counts by the dilution-plating method (following restoration of the flasks to volumes of 50 ml to replace evaporation losses) were made in triplicate.

The data are summarized in Table III. The following points are noteworthy: (1) vitamin supplements to the ashed TSE-25% B medium did not stimulate algal growth; (2) the least growth occurred in dim light in the ashed TSE-25% B medium, with and without vitamins; (3) about 29 times as much growth occurred in dim light in the unashed TSE-25% B medium as compared with the ashed cultures; (4) the greatest growth in dim light occurred in the ashed TSE-25% B medium enriched with glucose; (5) in bright light growth was poorest in unashed TSE-25% B medium but this growth was three times greater than that in the same medium in the dim light; (6) growth in ashed TSE-25% B medium in bright light with and without vitamins was greater than in the unashed medium in bright light; and (7) the greatest growth in bright light occurred in ashed TSE-25% B medium with glucose. The ashed TSE-25% B media enriched with glucose had reduced final pH, especially in the dim-light cultures.

TABLE III. Data from Experiment 1 on photoheterotrophism of *Bracteacoccus* A-20.

Medium and conditions	Final pH[4]	Macroscopic appearance	No. cells/ml.[4] x 10^4
B-glucose solution; bright light.....	7.5	dense, deep-green	300.0
Ashed TSE-25% B; bright light....	7.8	grass-green	15.8
Ashed TSE-25% B; dim light......	7.5	no visible growth	0.07
Ashed TSE-25% B, vitamins added; bright light..................	7.7	grass-green	17.8
Ashed TSE-25% B, vitamins added; dim light.....................	7.3	no visible growth	0.02
Unashed TSE-25% B; bright light..	7.7	green	6.0
Unashed TSE-25% B; dim light....	7.4	faint, dark-green growth on bottom	2.0
Ashed TSE-25% B, enriched with 0.20% glucose; bright light......	6.9	dense orange	150.0
Ashed TSE-25% B, enriched with 0.20% glucose; dim light........	5.7	pale, creamy yellow	300.0

[1] Averages of three flasks.

Experiment 2

This experiment was like the first with the following modifications: (1) vitamin supplements were omitted; (2) the inorganic salts composing the B solution were added directly from stock solutions resulting in 25% enrichment of the ashed and unashed TSE; (3) direct cell counts were made in lieu of the dilution-plating technique. For direct counts, cells were dispersed by scraping the walls of the culture vessels and shaking; a minimum of 10 separate fields was counted for each culture.

In Experiment 2 measurements of pH and microscopic observations were similar to those in Experiment 1. The data in Table IV (Experiment 2) are comparable to those in Table III (Experiment 1) and may be summarized in order with the results of this previous experiment. (2′) the least growth occurred in dim light in the ashed TSE-25% B medium; (3′) about 22 times as much growth occurred in dim light in the unashed TSE-25% B medium as compared with the ashed cultures; (4′) the greatest growth in dim light occurred in the ashed TSE-25% B medium enriched with glucose; (5′) in bright light growth was poorest in unashed TSE-25% B medium but this growth was 3 times greater than that in the same medium in dim light; (6′) growth in ashed TSE-

---

[3] Contents of vitamin mix (µg/L): thiamin, 10,000; biotin, 100; pantothenate, 10,000; cobalamine, 12. These were dissolved in distilled water containing 0.0175% KH_2PO_4 and then autoclaved.

25% B medium in bright light was greater than in the unashed medium grown under the same conditions; and (7′) the greatest growth in bright light occurred in ashed TSE-25% B medium with glucose. It was observed during the direct cell counts that algal cells were frequently clumped; this was especially pronounced in the illuminated cultures containing glucose.

TABLE IV. Data from Experiment 2 in photoheterotrophism of *Bracteacoccus* A-20

Medium and conditions	No. cells/ml. x 10^4	Avg. no. cells x 10^4	Range of difference between triplicate cultures (x 10^4)
Ashed TSE-25% B; bright light.	580.5 330.5 contaminated	455.5	250.0
Ashed TSE-25% B; dim light.	2.46 1.73 1.62	1.94	0.84
Unashed TSE-25% B; bright light.	96.7 166.3 98.9	120.6	69.6
Unashed TSE-25% B; dim light.	44.6 35.0 44.0	41.2	9.6
Ashed TSE-25% B, enriched with 0.20% glucose; bright light.	1,075 1,540 1,604	1,406.0	529.0
Ashed TSE-25% B, enriched with 0.20% glucose; dim light.	609.8 771.4 contaminated	690.6	161.6

DISCUSSION

Since the studies of Bristol-Roach (1926, et seq.), phycologists have been aware that some photoautotrophic soil algae are capable of a degree of heterotrophy (organotrophy). However, Petersen's (1935) review and the papers of Fritsch (1936) and John (1942) make it clear that although algae may grow heterotrophically in defined media of the laboratory there is no positive evidence of similar behavior in nature.

The preliminary investigations described here confirm the results of studies of Bristol-Roach (1927, 1928). They show that at least some soil algae can grow heterotrophically in the laboratory.

After more than one year of cultivation in total darkness a 16-fold increase in the number of cells of *Bracteacoccus* A-20 occurred in soil-water cultures when the alga was associated with a heterotrophic bacterium. In contrast, no increase in algal cell numbers was detected in cultures lacking the bacterial associate. This suggests that organic substrates for algal growth might be supplied by the heterotrophic bacterium. If this suggestion is valid, an interesting paradox is revealed.

Earlier reports of success in obtaining increases in algal cell numbers during long periods of dark cultivation in soil have been criticized on the basis of impure cultures. More recently efforts have been made to use pure cultures for such experimental studies; however, such pure cultures result in failure to obtain significant heterotrophic growth of algae in soil. This may signify that the absence of associated obligate heterotrophs accounts for the failure to demonstrate facultative heterotrophy by algae in soil. Consideration of this possibility in the light of modern concepts of soil microecology will help to clarify this idea.

The microenvironment of soil may be conceived as in a state of dynamic equilibrium such that normally no surplus of any simple substrate accumulates because it is acted upon instantly by various members of the soil community. In general, the more complex the substrate the longer the period required for its complete decomposition and dispersal within the soil community and the fewer the species capable of decomposing it. Under the artificial conditions of a pure culture in sterilized soil, certain substrates accumulate that would ordinarily be re-cycled by a more complete soil community. This is especially true in most algae where heterotrophy is not obligate and is probably of secondary importance to photoautotrophy. Their heterotrophic capabilities are usually less versatile and more limited to simple, common substrates (e.g., glucose, acetate, glycine, aspartate, glutamate) (Provasoli and Pintner 1960). Since these compounds are assimilated by a large number of organisms, it follows that their concentrations in natural soils ought to be limiting. Thus, soils will not have appreciable quantities of growth substrates for algae at any one instant, and pure culture studies involving algal heterotrophy will not support substantial increases in cell numbers in unenriched soil media. In contrast, obligate heterotrophs may be capable of the decomposition of more complex, more abundant substrates (e.g., chytins, celluloses, lignins, humic acids). As these compounds tend to be decomposed extracellularly at moderate rates, simplified dissimilation products are produced continuously in small amounts. If such products follow the normal pattern of diffusion, at least some substrate molecules may reach the cells of associated organisms in the soil community and be absorbed and assimilated. When an obligately heterotrophic bacterium is associated in soil-water culture with a facultatively heterotrophic alga, a continuous supply of substrates to one or both organisms may result. *Bracteacoccus* A-20 and bacterium B-6 seem to fit this hypothetical interpretation.

The comparative studies of algal growth in pure, ashed and unashed soil extract cultures in both dim and bright light augment the results from the 14-month experiment on heterotrophy in soil-water cultures. The hope that catalytic amounts of light would magnify the effects of trace quantities of available organic substrates disclosing a significantly enhanced growth of algae in the absence of the heterotrophic bacterium in a few weeks' time was realized repeatedly.

In Experiment 1, 29 times as many cells were detected by the dilution-plating method in unashed TSE-25% B medium as in the ashed TSE-25% B medium. In the second experiment, a 22-fold increase in the unashed TSE-25% B medium occurred, as shown by direct cell counts. The differences in the data with respect to ashed, dim- and unashed, dim-light cultures appear significant.

The importance of differences in availability to algae of carbon dioxide and bicarbonate in certain studies of heterotrophy has been stressed by Fogg (1953). It is unlikely that levels of fixable carbon limited algal growth in dim light in these experiments for growth in bright light was always much greater than that in dim light, except in glucose-enriched cultures. Similarly, differences in availability of ammoniacal vs. nitrate nitrogen between the ashed and unashed media could not account for the differences in growth observed because nitrogen was sufficient to allow 300 × 10^4 cells in some cultures, and Krauss (1958) has reported that no difference in growth occurs with either inorganic nitrogen source.

The possibility that certain B vitamins, rather than energy substrates, in exogenous supply in the soil extract stimulated algal growth (Rodhe 1948) is unlikely because (1) vitamin supplements did not improve growth in ashed media, (2) autoclaving the media, which had an initial pH of 7.5, is not conducive to the conservation of B vitamins, and (3) the improved growth of the alga in bright light as well as in darkness with glucose attests to its ability to supply adequately its own vitamin needs.

The best growth obtained in ashed TSE-25% B medium enriched with glucose is explained by the assimilation of this exogenous energy source concomitantly with photosynthetic assimilation. No claim is made that the bright illumination was saturating in these experiments. In fact, it was probably suboptimal in intensity, which would explain the enhanced growth in the presence of glucose. The fact that the poorest growth in bright light in both experiments occurred in the unashed TSE-25% media was due, no doubt, to the reduction in the light intensity with penetration through the yellowish soil extract. Up to 50% of the intensity of light (measured by a Weston Photronic Foot-Candle meter) is absorbed (or scattered) in penetrating the unashed TSE to a depth equivalent to the diameter of the medium in a 125 ml Erlenmeyer flask; in comparison, a negligible amount of light is lost in penetration through an equivalent depth of ashed TSE-25% B medium. There is little doubt that cell numbers in the unashed medium would have been greater had compensations been made for the light absorbed by the yellow pigments in the TSE; hence, the degree of photoheterotrophy may be greater than indicated by these experiments.

In Experiment 1, the glucose-enriched cultures in dim light contained approximately twice as many cells as cultures in bright light. The result was reversed in Experiment 2. This difference, if significant, is understood by the differences in the methods of each experiment for making cell counts. Microscopic studies showed that there was an increased tendency for cells to aggregate in cultures grown in bright light with glucose as compared with those grown in dim light with glucose. Presumably the higher rate of photosynthetic assimilation in the presence of exogenous sugar accompanies an increased production of extracellular polysaccharides in *Bracteacoccus* A-20 resulting in increased cellular aggregations. Thus, in the first experiment, which employed dilution-plating, some cell aggregations were counted as single cells, while in the second experiment, only individual cells were determined.

No attempt has been made to ascertain the cause of the reduction in pH which accompanied both dim and bright light growth of *Bracteacoccus* A-20 in glucose-salts media. The production of organic acids (Allen 1956, Sieburth 1960 and Fogg 1961) is a distinct possibility, and the yield may be substantial to account for the observed reduction in pH in this buffered medium.

These studies demonstrate that *Bracteacoccus* A-20 can grow, at least to some extent heterotrophically, in soil-water culture when associated with a suitable obligate heterotroph (i.e., bacterium B-6). *Bracteacoccus* A-20 is photoheterotrophic in pure soil extract cultures. These conclusions support the well-known hypothesis that heterotrophy (or organotrophy) and photoheterotrophy (or photo-organotrophy) may be accomplished by certain soil algae in their natural environment. The implications of such a capacity have been discussed adequately by Bristol-Roach (1926 et seq.) and Petersen (1935). It need be added only that some evidence now exists for the idea that certain algae found alive at depths of more than one meter in soil actually may be growing in perpetual darkness.

SUMMARY

A study was made to ascertain whether heterotrophy and photoheterotrophy by algae were possible in media containing soil or soil extract from the natural habitat of the algae as the sole source of carbon substrates. A routine survey of heterotrophic capabilities of 12 recent soil isolates was conducted in defined glucose-salts medium. These were 6 species of *Bracteacoccus,* 2 of *Neochloris,* 2 of *Chlamydomonas,* one species of *Phormidium,* and one of *Hantzschia.* The 8 species in the first 2 genera, all chlorococcalean algae, grew heterotrophically in the defined medium, while the others did not. One of these presumptive natural heterotrophs, *Bracteacoccus* A-20, was cultivated in soil-water medium in total darkness for more than one year. Algal cell numbers increased only when associated with an obligately heterotrophic bacterium under these conditions. This same alga increased significantly in pure cultures when grown in unashed soil extract media as compared with ashed media, both at very low light intensities. The results appear to support the hypothesis that heterotrophy and photoheterotrophy by algae do occur in soil.

REFERENCES

Allen, M. B. 1956. Excretion of organic compounds by *Chlamydomonas.* Arch. Mikrobiol. **24:** 163-168.

Bold, H. C. 1949. The morphology of *Chlamydomonas chlamydogama,* sp. nov. Bull. Torrey Bot. Club **76:** 101-108.

Belcher, J. H. and J. D. A. Miller. 1960. Studies on the growth of Xanthophyceae in pure culture. IV. Nutritional types amongst the Xanthophyceae. Archiv. f.Mikrobiol. **36:** 219-228.

Bristol-Roach, B. M. 1926. On the relation of certain soil algae to some soluble organic compounds. Ann. Botany **40:** 149-201.

———. 1927. On the carbon nutrition of some algae isolated from soil. Ann. Botany **41:** 509-517.

———. 1928. On the influence of light and of glucose on the growth of a soil alga. Ann. Botany **42:** 317-345.

Fogg, G. E. 1953. The metabolism of algae. John Wiley and Sons, Inc., New York.

———. 1961. The extracellular products of algae. Physiology and Biochemistry of Algae., Lewin (ed.), Academic Press, N. Y.

Fritsch, F. E. 1936. The role of the terrestrial alga in nature. Essays in Geobot. in Honour of W. A. Setchell: 195.

John, R. P. 1942. An ecological and taxonomic study of the surface-growing algae. I. Distribution of the surface-growing algae. Ann. Bot. (N.S.) **6:** 323-349.

Killam, A. and J. Meyers. 1956. A special effect of light on the growth of *Chlorella vulgaris.* Amer. Jour. Bot. **43:** 569-572.

Krauss, R. E. 1958. Physiology of fresh-water algae. Ann. Rev. Plant Physiol. **9:** 207-244.

Lewin, J. C. 1953. Heterotrophy in diatoms. J. Genl. Microbiol. **9:** 305-313.

Lewin, J. C. and R. A. Lewin. 1960. Auxotrophy and heterotrophy in marine littoral diatoms. Canadian J. Microbiol. **6:** 127-134.

Myers, J. 1951. Physiology of algae. Ann. Rev. Microbiol. **5:** 157-180.

Palmer, C. M. 1959. Algae in water supplies, illustrated manual on identification, significance, and control of algae in water supplies. Robert A. Taft Sanitary Engineering Center, Cincinnati, Ohio, 1-88.

Petersen, J. B. 1935. Studies on the biology and taxonomy of soil algae. Dansk. Bot. Ark. **8:** 1-183.

Provasoli, L. and I. J. Pintner. 1960. Artificial media for fresh-water algae: Problems and suggestions. The Ecology of Algae (Pymatuning Symp. in Ecol., Spec. Publ. No. **2:** 84-96. Univ. Pittsburgh, Pittsburgh, Penna.

Pruess, L., P. Arnow, L. Walcott, N. Bohonos, J. J. Oleson, and J. H. Williams. 1954. Studies on the mass culture of various algae in carboys and deep-tank fermentations. Appl. Microbiol. **2:** 125-130.

Rodhe, W. 1948. Environmental requirements of frĕsh-water plankton algae. Experimental studies in the ecology of phytoplankton. Symb. Bot. Upsaliensis **10:** 1-149.

Saunders, G. W. 1957. Interrelations of dissolved organic matter and phytoplankton. Bot. Rev. **23:** 389-409.

Sieburth, J. M. 1960. Acrylic acid, an "antibiotic" principle in *Phaeocystis* blooms in Antarctic waters. Science **132:** 676-677.

THE PLANT ECOLOGY OF THE TEAK PLANTATIONS IN TRINIDAD

PHILIP ROSS
Potomac, Maryland

INTRODUCTION

Teak plantations were first established in Trinidad in 1913 when Burmese teak seeds were planted in the Southern Watershed Reserve. Small areas were planted each succeeding year until 1928 when a definite teak plantation program was established. In 1936 the Forest Department formulated a general plan for teak plantations calling for the planting of 800 acres per annum. By 1956, teak plantations covered 10,121 acres.

This paper is the result of an investigation of plants that have invaded the plantations, the plant succession involved, and the environmental factors affecting the establishment of an understory of natural vegetation at the 3 major centers of teak plantations: Mount Harris and Brickfield in the Central Range Reserve, and the Southern Watershed Reserve. The introduction of an exotic plant, such as teak, brings about changes in environmental conditions, such as temperature and moisture, which also affect the development of the understory. With the establishment of plantations, fire has become an important factor in influencing environmental change.

Teak, *Tectona grandis* L.f., is indigenous throughout Burma, the Indian Peninsula, and the islands of the Indian Archipelago, where it occurs normally in the mixed deciduous forest. Trinidad teak plantations are established by the Burma taungya system. Local men sign a contract with the Forest Department under which they are allowed use of the land rent-free for 15 months to plant food crops; in return they must clear the land of the natural forest, keep it free from weeds, and tend teak stump plants which are set out in the field from the nursery. The forested area surveyed for the teak plantation is cut by contractors in January and February. Smaller trees are utilized by charcoal burners who set up "pits" in the area. The remaining vegetation is burned usually in March or April during the dry season. Teak stump plants from the nursery are planted in rows 6 ft apart during May and June by the contractor. Figure 1 shows the nursery which will supply stump plants for the 1958 Coupe in the Southern Watershed Reserve. During the next 15 months, or until the teak overgrows and shades out their food crops, the contractors raise corn, hill rice, dasheen, cassava, and pigeon peas. Upon harvesting of the food crops the plantation is cleared and turned over to the Forest Department for management. Yearly plantings of teak are called "coupes." Teak plantations are thinned every 5 yrs and during the first thinning half the original 1200 trees per acre are removed. By the time the trees reach maturity in 60-80 yrs, approximately 50 trees per acre are left standing. For a more complete description of the establishment of teak plantations in Trinidad see Ross (1959).

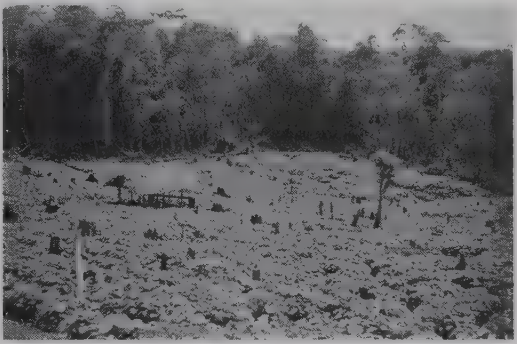

FIG. 1. Southern Watershed Reserve, Western Felling Series. Teak nursery which will supply stump plants for the 1958 coupe. Teak seedlings in the picture are 5 months old.

ENVIRONMENTAL CONDITIONS IN TRINIDAD AND REQUIREMENTS OF TEAK

Topography

Trinidad, the most southerly of the West Indian islands, is roughly rectangular, about 50 miles long from north to south, and about 32 miles wide from east to west in its central part. Its total area is 1,862 sq miles. The northwestern promontory of Trinidad and a group of small islands are separated by approximately 7 miles from Venezuela on the mainland of South America. Geologically, Trinidad conforms with the structure of the Venezuelan coast. Because of its geographical position it has a large South American element in its flora which separates it biologically from the other Caribbean islands.

Trinidad is divided into 5 topographical regions formed by 3 ranges of hills and the intervening

---

[1] The research was undertaken while the author was studying at the Imperial College of Tropical Agriculture under the auspices of a Fulbright grant. The author wishes to express his sincere appreciation for the kind and considerate assistance of Mr. David Moore, Conservator of Forests, Trinidad, and his staff, especially Messrs. Inchbold-Stevens, Bain, Frost, and Joseph.

lowlands (Hardy 1956). The Northern Range composed of metamorphic schists forms an extension of the coastal cordillera of Venezuela with a general elevation over 500 ft and a maximum height at El Cerro del Aripo, 3,083 ft, and El Tucuche 3,072 ft. Numerous transverse valleys have steep to precipitous slopes.

The Northern Plain, south of the Northern Range, at 100 ft, stretches across the Island from the Caroni Swamp on the west coast to the east coast. The plain is composed mainly of recent alluvial deposits and older sands and gravels. Its southern edge is limited by the Central Range of hills that run in a northeast direction from Pointe à Pierre on the west to Manzanilla on the east. Mt. Tamana, reaching 1,008 ft in the center of the island, is the highest point of these rolling hills. The hills are generally composed of silt and clay but are flanked to the north with beds of sand. South of the Central Range there extends a wide zone of sandy lowlands with an elevation of 200 ft comprising the Nariva Swamp in the east and rolling country in the west. The Southern Range of hills runs westward along the coast from the Trinity Hills, 997 ft in the southeast, and is composed mainly of clays.

Undulating land is best suited to teak plantations because the slopes usually provide the free drainage which is absolutely essential. Gentle slopes are often good sites when natural drainage is supplemented by artificial drainage ditches. Teak plantations in Trinidad are located primarily on the rolling hills of the Central Range, but the undulating Southern Range of hills also supports successful plantations.

Soils

Since Trinidad is structurally a part of the South American continent, its soils are not like those of other West Indian Islands which have developed upon a coral or volcanic base. Hardy (1956) has classified the soils of Trinidad into 5 main groups:

I. Hydromorphic Soils, occupying 41% of land surface
II. Calcimorphic brown forest soils, occupying 2% of land surface
III. Latosols and Tropical Podzolic Soils, occupying 26%
IV. Regosol, occupying 29%
V. Alluvial Soils, occupying 2%

Teak will tolerate wide extremes in soils if drainage is adequate. Teak trees showing the highest rate of height and girth growth are on fertile calcareous clays, but successful plantations are also on soils with 95% sand to heavy clays. Flat-topped ridges with a hard, compact clay soil and flat areas with shallow sand beds overlying clay are unfit for teak. The following discussion of soil types is summarized from Chenery (1952). Soils at the 3 centers of teak plantations are mostly Hydromorphic Soils. Mount Harris catena at Mount Harris in the Central Range Reserve, Naparima clay at the Southern Watershed Reserve, and Talparo clay at Brickfield in the Central Range Reserve are all non-calcareous perched gley soils. Tarouba clay at Brickfield is also a perched gley, with a calcareous parent material. The only non-perched gley soil under teak plantations is the Moruga loam in the Southern Watershed Reserve which is classified as a regosol because there are no clearly developed soil characteristics.

Climate

The climate in Trinidad is controlled by the periodicity of rainfall (Table I). The rainy season from May to December may be interrupted by the "petite carême," a short dry season in September and October, but the true dry season is from January to April or May.

During the dry season a minimum temperature below 65°F is not uncommon and the maximum temperature seldom exceeds 86°F. The driest months (February, March, and April) average less than 2 in. of rainfall.

During the rainy season minimum temperatures below 72°F are seldom recorded. Wet day maximum temperatures often exceed 90°F. May is the hottest month, averaging 89.8°F. June, July, and August are the 3 wettest months, each averaging 8 in. or more of rainfall. Nearly all of Trinidad is climatically suitable for teak, which thrives best in a moist, warm tropical climate.

Precipitation and its periodicity are important factors for growth of teak. Analysis of these factors at the 3 centers of teak plantations are from

TABLE I. Average precipitation for the three study areas

Station	Years	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Mount Harris........	20	7.58	5.14	4.21	4.90	9.46	14.19	12.35	13.20	9.65	10.73	12.90	13.74	118.05
Brickfield............	13	5.30	4.02	2.39	2.74	8.20	14.10	11.40	12.40	6.73	7.65	9.64	10.07	94.64
Southern Watershed Reserve..........	20	4.40	2.01	2.17	2.20	4.82	8.55	8.16	9.28	5.31	5.02	7.07	6.75	65.74

rainfall data which have been published by Wehekind and Smith (1953) and Bain (1934). The data show a decrease in precipitation from north to south. Mount Harris, where rainfall has been recorded for 20 yrs, has an average yearly precipitation of 118.05 in. June, which has an average of 14.19 in. of rain, is the wettest month. July, August, November, and December all have monthly averages over 12 in. March, which averages 4.21 in., is the driest month. Because of the variation in rainfall from year to year during the driest month which also varies, Mount Harris is not considered to have a rain forest climate.

Brickfield precipitation data show a distribution pattern similar to Mount Harris although drier. The total average annual rainfall for 13 yrs is 94.64 in. June is again the wettest month, having 14.10 in. of rain, and March is the driest month with 2.39 in. The average monthly precipitation during March and April is less than 3 in.

The Southern Watershed Reserve is the driest of the 3 centers of teak plantations. The total annual precipitation for 20 yrs is 65.74 in. The wettest month is August, which averages 9.28 in. of rain, and the driest month is February, which averages 2.01 in. February, March, and April have average precipitation under 3 in.

Plant Distribution in the Teak Plantation

Methods of analysis

Three centers of teak plantations were selected for study: Mount Harris Felling Series, with plantations among the most northerly on the island, is in an area with over 100 in. of rain; Brickfield Felling Series is in the center of the island and is the largest area under teak; the Western Felling Series of the Southern Watershed Reserve, one of the most southerly areas of teak, is one of the driest and includes some of the oldest plantations. Figure 2 shows the location of the 3 Forest Reserves and their relation to the vegetation of Trinidad.

Teak coupes in 5 yr intervals from the youngest to the oldest were studied to compile a list of plants which have become established in plantations at the 3 selected areas and to interpret their role in the successional pattern of vegetation. For adequate sampling of the vegetation of each coupe, the sample size must be equal to, but preferably greater than, the size of the minimal area of vegetation in each coupe. In the tropical rain forest with its great wealth of species an adequate sample plot size is necessarily large. Richards (1939) found that 160,000 sq ft in a mixed rain forest in southwestern Nigeria was smaller than the minimal area for trees 4 in. in diameter and larger. Greig-Smith (1952), in a study of the degraded secondary forest in Trinidad, stated that his sample area, 100 plots each 25 sq ft, was too small for an adequate assessment of the species. He based this assumption on the fact that the species-area curves for the full sample area were still rising sharply. Van Steenis (1958b) suggests that because of the complexity of vegetation in a tropical rain forest, the minimum area is too large to be practical for sampling. Since secondary herbaceous and shrubby vegetation is less uniform in distribution than original vegetation, quadrat sampling was not considered adequate for gathering information on vegetation in teak coupes. Four times during the year the vegetation of the entire coupe was studied in detail by transects 5 m apart running the length of the coupe. Species were listed and then scaled (r — 5) for cover degree-abundance (Table II) and (.1 — .5) for sociability. This system is similar to that of Braun-Blanquet (1932).

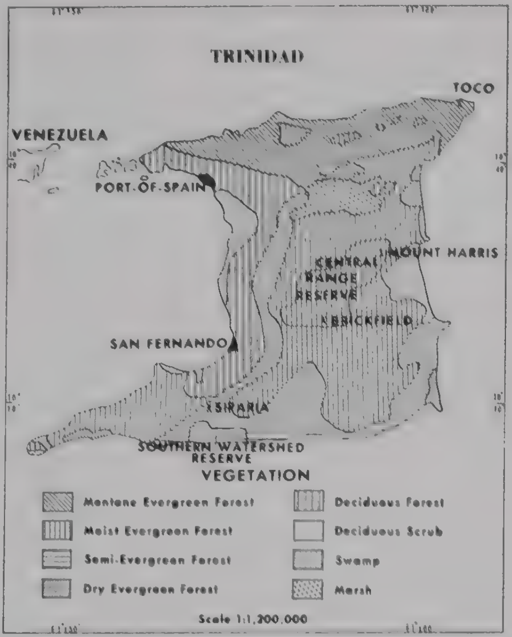

Fig. 2. Vegetation types of Trinidad and Forest Reserve study areas.

The list of plants in each coupe was made with the assistance of a native forest ranger from the Forest Department and checked with Marshall (1939), Beard (1946), and with Williams (1928). I collected and identified many herbaceous and shrubby plants in the teak coupes and these specimens are in the herbarium at the Imperial College of Tropical Agriculture.

TABLE II. Scales of combined cover degree-abundance and sociability

Combined cover degree-abundance	Sociability
r erratic occurrence	.1 solitary individuals
+ occasional, less than 5% cover	.2 small groups of few individuals
1 abundant, less than 5% cover	
2 abundant, 5-25% cover	.3 large groups of many individuals
3 abundant, 25-50% cover	
4 abundant, 50-75% cover	.4 large patches
5 abundant, 75% or greater cover	.5 extensive mat

Natural Vegetation

To establish a background for discussion of distribution of plant species in the plantations, a brief survey of the natural vegetation of Trinidad is included (Fig. 2). The reader is referred to Beard (1946) for a more comprehensive discussion.

The vegetation of Trinidad has been disturbed by man through cutting and fire, but the general structure and composition of the communities have not been seriously altered. Sugar cane fields have replaced forests on the flat to rolling land in the central part, and cocoa, citrus and coffee plantations are scattered in the valleys and on hillsides in the northern mountains. Selective cutting of valuable timber trees throughout the Island has reached all but the most inaccessible forests. The remaining vegetation is classified as Broadleaf Evergreen Forest, Broadleaf Deciduous Forest, Swamp Forest, and Marsh.

The Broadleaf Evergreen Forest, in which canopy less than half of the trees are deciduous, has *Carapa guianensis* and *Eschweilera subglandulosa* as major species. *Mora excelsa,* occurring in pure stands in this forest type, is considered a special faciation. Two of the plantation sites, Mount Harris and Brickfield, are located in this vegetation type which occupies the central and southeastern sections of Trinidad. As the deciduous component in the canopy increases, 2 other associations are identifiable. The first is characterized by *Peltogyne porphyrocardia,* and the second by *Trichilia smithii* and *Brosimum alicastrum.* The Southern Watershed Reserve is within the latter association. A stunted broadleaf evergreen forest, scattered along the drier east coast and influenced by trade winds and salt spray, has an association of *Coccoloba uvifera-Hippomane mancinella* on the exposed coastline and one of *Roystonea oleracea-Manilkara bidentata* inland.

The rich evergreen montaine forest of the northern range of mountains is characterized by a *Byrsonima spicata* and *Licania ternatensis* association from 800-2500 ft, and an association of *Richeria grandis* and *Eschweilera* spp. up to the summit of El Aripo. The summit is covered by a stunted, gnarled deciduous scrub of *Clusia intertexta.*

The Broadleaf Deciduous Forest, in which over 2/3 of the forest canopy individuals are deciduous, is represented by a faciation of *Machaerium robinifolium.* This forest is in the drier northwest section of the country where the original *Bursera-Lonchocarpus* association has been eliminated by human interference.

Extensive areas on both east and west coasts are covered by a brackish water Swamp Forest of mangrove trees of *Rhizophora mangle, Avicennia nitida* and *Laguncularia racemosa* and by a dense fresh water Swamp Forest of *Roystonea oleracea, Mauritia setigera,* and *Pterocarpus officinalis.*

Marsh vegetation has developed on flat alluvial terraces which undergo a dry and wet season and is characterized by *Cyperus giganteus, Gynerium sagittatum, and Montrichardia arborescens.*

Mount Harris is in the widespread Broadleaf Evergreen Forest in which *Carapa guianensis* and *Eschweilera subglandulosa* are characteristic species. The local plant association has been named after *Pentaclethra macroloba* and *Maximiliana elegans,* which are common in the area. Other common tree species include *Aniba panurensis, A. trinitatis, Licania biglandulosa, Fagara martinicensis,* and *F. trinitensis.* The trees form a canopy from 50-70 ft high, but emergents often reach over 100 ft. Lianes and epiphytes are abundant on larger trees. The shrub layer is well developed with species such as *Miconia* spp., *Piper* spp., *Inga* spp., *Eugenia confusa, Psychotria cuspidata,* and *Ryania speciosa.* Herbaceous vegetation is scarce because of shading by dense overhead vegetation.

Teak plantations at Mount Harris (Table III) have been established on the eastern slopes of the hill. A heavy undergrowth of shrubs, vines, and herbaceous plants has developed under the teak in the 1954 coupe on the southeast slope of Mount Harris. The 1949 coupe has little undergrowth because fire during the past 2 yrs has destroyed the vegetation. During 1953 and 1948, teak coupes were not planted at Mount Harris. The teak trees in the 1943 coupe have a partially closed canopy. Shrubs are well developed, and the ground is sparsely covered with herbaceous vegetation. The 1938 coupe has a heavy undergrowth of shrubs and teak coppice shoots.

Because of heavy rainfall at Mount Harris, shrubs soon invade newly established teak coupes and shade out grasses and herbaceous vegetation. Only a few light-demanding plant species were found in the 1954 coupe: *Cecropia peltata, Asclepias curassavica, Solanum hirtum, Bidens pilosa,* and *Acnistus arborescens.* The following plants

TABLE III. Synthesis table for the vegetation of the teak coupes in the Central Range Reserve, Mount Harris Felling Series

		Natural Vegetation	1938 Coupe	1943 Coupe	1949 Coupe	1954 Coupe
	Acres		21	11	20	16
	Topography		slight NE slope	steep SE slope	slight N slope	steep SE slope
	Elevation		100-200 ft.	200-300 ft.	100-150 ft.	300-400 ft.
Teak Trees	No./acre		360	400	550	1200
	Height		45-50 ft.	30-35 ft.	25-30 ft.	15-18 ft.
	D.B.H.		10-15 ins.	8-10 ins.	4-6 ins.	4-5 ins.
		Combined Cover Degree—abundance and Sociability				
Trees—single stem woody plants over 15 ft. high						
Aniba panurensis Mez		+ .1				
Aniba trinitatis (Meissen.) Mez		+ .1				
Bravaisia integerrima (Spreng.) Standl		1.1				
Brownea latifolia Jacq		1.1	+ .1	+ .2	+ .1	1.2
Calophyllum lucidum Benth				+ .1		
Carapa guianensis Aubl		1.1	1.1	+ .1		
Cecropia peltata L						+ .1
Diospyros ierensis Britt		1.1				
Eschweilera subglandulosa (Steud.)		2.1	1.1	+ .1		
Eugenia confusa DC		1.2				
Fagara martinicensis Lam		1.1	+ .1	+ .1		
Fagara trinitensis (Williams) J. S. Beard		1.1				1.1
Hieronyma caribaea Urb		1.1		+ .1		
Inga laurina (Sw.) Willd		1.1			1.1	
Inga venosa Griesb. ex. Benth		1.1	+ .1			2.2
Licania biglandulosa Griesb		1.1				
Myrica spp. Wild Guava		1.2				
Pachira insignis Sw		1.1				
Pentaclethra macroloba (Willd.) Kuntze		3.2	2.1	2.1	+ .1	2.1
Sterculia caribaea R. Br		1.1				
Vismia cayennensis Pers			1.2	1.2	+ .1	1.2
Vismia falcata Rusby			+ .2			
Shrubs—multiple stem woody plants under 15 ft. high						
Achistus arborescens (L.) Schlecht						1.2
Cassia fruticosa Mill		+ .1	+ .1			
Cephaelis tomentosa Willd				+ .1		
Clidemia dependens D. Don				1.3		1.2
Clidemia hirta (L.) D. Don				+ .1		
Duggena hirsuta (Jacq.) Britton			1.1	+ .2		2.2
Flemingia strobilifera R. Br			1.2			
Leandra rufescens (DC.) Cogn			+ .1			
Miconia acinodendrum (L.) Triana		1.1	+ .1			
Miconia ciliata (Rich.) DC		+ .1		1.2		
Miconia nervosa (Smith) Triana		1.2	1.2			
Miconia racemosa (Aubl.) DC				+ .1		
Piper aequale Vahl						1.2
Piper hispidum Sw		+ .1	+ .1		1.2	
Pothomorphe peltata (L.) Miq						1.2
Psychotria cuspidata Bred		+ .2	1.1	1.2		
Ryania speciosa Vahl		+ .1	1.2	+ .1		
Solanum hirtum Vahl						+ .1
Solanum subinerme Jacq			+ .1			
Warszewiczia coccinea (Vahl) Kl		1.2				
Herbaceous plants						
Asclepias curassavica L						1.2
Bidens pilosa L						+ .2
Blechum brownei Juss				+ .1		
Borreria verticillata (L.) Meyer			+ .2			+ .1
Calathea lutea (Aubl.) Meyer			+ .2		1.2	1.2
Centropogon surinamensis (L.) Presl			+ .1			
Costus cylindricus (Plum.) Jacq			+ .1			+ .1
Cyalthula achyranthoides (H.B.H.) Moq				+ .2		
Cyperus luzulae (L.) Retz				+ .2		1.2
Heliconia bihai L		2.3	1.2	2.3	2.2	2.3
Heliconia hirsuta L.f		1.2	1.2		+ .1	1.2
Ischnosiphon arouma Feinte		+ .2	+ .2	1.2		
Lisianthus chelonoides L.f			+ .1			
Nepsera aquatica (Aubl.) Naud			+ .1			
Pachystachys coccinea (Aubl.) Nees		+ .1	+ .2		+ .1	
Renealmia exaltata L.f		+ .2				
Rolandra fruticosa (L.) Kuntze		+ .1				

(Table III. Continued)

Teak Trees		Natural Vegetation	1938 Coupe	1943 Coupe	1949 Coupe	1954 Coupe
	Acres		21	11	20	16
	Topography		slight NE slope	steep SE slope	slight N slope	steep SE slope
	Elevation		100-200 ft.	200-300 ft.	100-150 ft.	300-400 ft.
	No./acre		360	400	550	1200
	Height		45-50 ft.	30-35 ft.	25-30 ft.	15-18 ft.
	D.B.H.		10-15 ins.	8-10 ins.	4-6 ins.	4-5 ins.
		Combined Cover Degree—abundance and Sociability				
Scleria arundinacea Kunth			+ .1	1.2	1.2	1.2
Tibouchina longifolia (Vahl) Baill.		1.2	+ .1	+ .1		
Palms						
Bactris spp.		1.2	1.2	1.2	+ .2	
Desmoncus major Bailey			+ .1	+ .1	+ .1	1.2
Maximiliana elegans Karst.		2.1		1.2		
Lianas						
Ipomoea tiliacea (Willd.)				+ .2		
Paullinia pinnata L.				+ .1		+ .1

were observed only in the 1938 coupe in other plantations: *Centropogon surinamensis, Leandra rufescens, Miconia* spp., *Lisianthus chelonoides,* and *Flemingia strobilifera.* With the exception of the last species, these are usually found in more moist areas of the natural forest. *Pentaclethra macroloba, Brownea latifolia, Heliconia bihai,* and *Vismia cayennensis* were found in all plantations. Fruits of these plants are eaten by birds and bats and seeds are widely distributed. *Aniba* spp. and *Licania biglandulosa,* common in the natural vegetation, had not become established in any of the plantations.

Central Range Reserve, Brickfield Felling Series

The natural vegetation in the Brickfield area (Table IV) is also a Broadleaf Evergreen Forest. Emergent trees such as *Carapa guianensis, Eschweilera subglandulosa,* and *Pachira insignis* are often over 100 ft high. A general canopy layer 50-80 ft above ground is formed by *Pentaclethra macroloba, Sabal* spp., and *Trichili smithii.* Vegetation is dense and lianes and palms are common. *Inga* spp. are commonly found on drier ridges along with *Fagara* spp., *Mouriri rhizophorifolia,* and *Vitex divaricata.* The shrub layer is dense and represented by species of *Miconia* spp., *Ryania speciosa, Duggena hirsuta,* and by tree seedlings. The herbaceous layer is restricted by the dense growth overhead to shade and moisture tolerant species such as *Heliconia bihai, Ischnosiphon arouma,* and *Calathea lutea.*

The teak coupes at Brickfield are planted primarily along the sides of a sandy ridge. Figure 3 shows the open condition and dense undergrowth of grass and other herbs in a recently established plantation. The 1953 coupe on a north slope was burned in 1957, opening the dense undergrowth for the invasion of grasses (Fig. 4). The 1948 coupe on a north slope has also been burned in past years. Because of the partial closing of the canopy, grasses have not invaded this coupe as in the 1953 coupe. The 1943 coupe, along the top of the sandy ridge, has not been burned for 3 or 4 yrs and shows good development of shrubs and herbaceous vegetation. Teak trees in this coupe have been invaded by parasitic bird vines (Loranthaceae: *Phorodendron* spp., *Phithirusa* spp., *Struthanthus* spp.). Plants found only in the 1953 teak coupe were typically light-demanding ones. They included *Bidens pilosa, Cordia panamensis, Cynodon dactylon, Maranta gibba,* and *Pterolepis glomerata.* Since the 1948 coupe had a partially closed canopy, grasses had died out and shrubs and more moisture-tolerant species of herbaceous vegetation had taken over (Fig. 5). In the 3 coupes studied, the most common plants were those with fruit which is eaten by birds and bats. These included *Vismia cayennensis, Eugenia confusa, Flemingia strobilifera, Manicaria saccifera, Sabal* spp., and *Miconia* spp.

The 1943 coupe still shows effects of earlier stages of plantation development when natural vegetation is cut and burned. This is an example of habitat desiccation which follows disturbance of natural vegetation in the tropics (Greig-Smith 1952). Plant species in this coupe are predominantly found in drier situations in the natural vegetation. *Pentaclethra macroloba, Pachystachys coccinea, Aniba* spp., *Pachira insignis,* and *Licania biglandulosa* were observed in the more moist natural vegetation nearby but not in any of the plantations.

TABLE IV. Synthesis table for the vegetation of the teak coupes in the Central Range Reserve, Brickfield Felling Series

Teak Trees	Natural Vegetation	1943 Coupe	1948 Coupe	1953 Coupe
Acres		115	150	250
Topography		Flat ridge top	steep N slope	slight N slope
Elevation		200-250 ft.	150-175 ft.	200-250 ft.
No./acre		400	600	1200
Height		35-40 ft.	25-30 ft.	10-15 ft.
D.B.H.		8-10 ins.	4-6 ins.	3-4 ins.
	Combined Cover Degree-abundance and Sociability			
Trees—single stem woody plants over 15 ft. high				
Aniba spp.	1.1			
Andira inermis (Wright) H.B.K.		+ .1	1.1	
Bravaisia integerrima (Spreng.) Standl.	1.1	1.1		
Brownea latifolia Jacq.	+ .1	+ .1	+ .1	
Bumelia Grisebachii Pierre	1.1			
Byrsonima spicata (Cav.) Rich.	+ .1			
Carapa guianensis Aubl.	1.1			
Cecropia peltata L.	2.1			
Cedrela mexicana Roem.	1.1	1.1	+ .1	
Ceiba occidentalis (Spreng.) Burkill	+ .1			
Chrysophyllum argenteum Jacq.	+ .1			
Clathrotropis brachypetala (Tul.) Kleinh.	+ .1			
Coccoloba fallax Lindau	1.1			
Cordia panamensis Riley				+ .1
Eschweilera subglandulosa (Steud.) Miers	1.1			
Eugenia confusa DC.		2.2	2.2	1.2
Fagara martinicensis Lam.	1.1	2.1	2.1	1.1
Fagara trinitensis (Williams) J. S. Beard	+ .1	1.1		
Guarea guara (Jacq.) P. Wilson	+ .1			
Guazuma ulmifolia Lam.	+ .1			
Inga ingoides (Rich.) Willd.	2.1	1.1		+ .1
Inga venosa Griesb. ex. Benth.	2.1	1.1		
Licania biglandulosa Griesb.	1.1			
Machaerium robinifolium (DC.) Vogel			+ .1	
Manilkara bidentata (A.DC.) Chev.	+ .1			
Mouriri rhizophorifolia (DC.) Triana	1.1			
Ocotea oblonga (Meissen.) Mez	+ .1			
Ocotea eggersiana Mez	+ .1			
Pachira insignis Sw.	+ .1			
Pentaclethra macroloba (Willd.) Kuntze	1.1			
Pisonia cuspidata Heimerl	1.1	+ .1	+ .1	
Platymiscium trinitatis Benth.	+ .1			
Pterocarpus rohrii Vahl		1.1		
Rollinia multiflora Splitz.		+ .1		
Rudgea freemani Sprague and Williams		1.1		
Sapium aucuparium Jacq.	1.1	+ .1	+ .1	
Spondias mombin L.	+ .1			
Sterculia caribaea R. Br.	+ .1		1.1	
Tabebuia rufescens J. R. Johnst.		+ .1	+ .1	+ .1
Trichilia smithii C.DC.	1.1			
Vismia cayennensis (Jacq.) Pers.		2.2	2.2	1.2
Vitex divaricata Sw.	+ .1			
Shrubs—multiple stem woody plants under 15 ft. high				
Acnistus arborescens (L.) Schlecht.	1.2	+ .1	+ .1	
Basanacantha phyllosepala Sprague and Williams	+ .1		1.1	
Cassia fruticosa Mill.		+ .1		
Cestrum latifolium Lam.		1.1		
Clibadium surinamense L.	+ .1			
Clidemia hirta (L.) D. Don			+ .1	
Duggena hirsuta (Jacq.) Britton	1.1	2.1		+ .1
Flemingia strobilifera R. Br.	+ .1	+ .2	1.1	1.3
Lantana camera L.		1.1		+ .1
Miconia acinodendrum (L.) Triana	1.2	2.2	1.1	
Miconia ciliata (Rich.) DC.		1.1		
Miconia racemosa (Aubl.) DC.	+ .1		1.2	
Piper glabresans (Mig.) D.DC.	+ .1			
Piper hispidum Sw.	1.1	+ .2	1.1	+ .2
Piper marginatum Jacq.				1.1
Ryania speciosa Vahl	+ .1		1.1	
Solanum hirtum Vahl		1.2		1.2

(Table IV. Continued)

		Natural Vegetation	1943 Coupe	1948 Coupe	1953 Coupe
	Acres		115	150	250
	Topography		Flat ridge top	steep N slope	slight N slope
	Elevation		200-250 ft.	150-175 ft.	200-250 ft.
Teak Trees	No./acre		400	600	1200
	Height		35-40 ft.	25-30 ft.	10-15 ft.
	D.B.H.		8-10 ins.	4-6 ins.	3-4 ins.
		Combined Cover Degree-abundance and Sociability			
Herbaceous plants					
Asclepias curassavica L. Matac			1.1		+ .3
Axonopus compressus (Swartz) Beauv					3.4
Bidens pilosa L					+ .2
Blechum brownei Juss				1.1	1.1
Borreria verticillata (L.) Meyer			1.2	+ .1	1.2
Calathea lutea (Aubl.) Meyer		1.2	+ .2	1.2	
Centropogon surinamensis (L.) Presl			+ .1		
Costus cylindricus (Plum.) Jacq		1.1			+ .1
Cyathula achyranthoides (H.B.H.) Moq				+ .1	
Cynodon dactylon (L.) Pers					1.1
Cyperus luzulae (L.) Retz			1.3		1.2
Heliconia bihai L		3.3	1.3	1.1	1.3
Hemidiodia ocimifolia (Willd.) K. Schum					+ .1
Hyptis capitata Jacq			1.2		1.2
Ischnosiphon arouma Feinte		1.2	1.2	1.3	1.2
Maranta gibba Sm					1.2
Mimosa pudica L			1.2		
Pachystachys coccinea Nees		+ .2			
Paspalum virgatum L			2.2		1.2
Pterolepis glomerata (Rottb.) Miq					+ .1
Rottboellia exaltata L.f					+ .1
Scleria arundinacea Kunth			1.2	+ .2	1.2
Palms					
Bactris spp		2.3	+ .1		
Desmoncus major Bailey		+ .2	2.2		
Manicaria saccifera Gaertn			3.3	1.2	3.3
Maximiliana elegans Karst		1.1			
Sabal spp		2.3	2.2	1.2	1.2
Lianas					
Dioclea reflexa Hook				1.2	+ .1
Paullinia faciculata Radlk			+ .1		

Southern Watershed Reserve, Western Felling Series

A drier and more open vegetation type of the Broadleaf Evergreen Forest has developed along the southern coast of Trinidad in which *Trichilia trinitensis* and *Brosimum alicastrum* are significant species. Other common tree species are *Bravaisia integerrima, Sabal* spp., and *Machaerium robinifolium.* The lower rainfall (65 in.), exposure to sea winds, and the impermeable Naparima Red Clays are main factors controlling growth of vegetation. The ground tends to be wet during the rainy season but quickly dries with the approach of the dry season. Primary vegetation forms a patchy canopy from 50-75 ft, while a continuous lower canopy is developed between 20-30 ft above ground.

Many vines cover the crowns of larger trees. *Anodendron paniculatum,* the rope vine, and *Gouania lupuloides,* the tooth brush vine, are common. Shrubby vegetation is well developed especially under openings in the canopy. *Bactris* spp., *Psychotria cuspidata, Piper* spp., and small trees are abundant. Herbaceous vegetation is scarce. The steep south-facing slope of the 5-yr-old teak coupe, 1953, at Quarry Road is covered by grasses and herbs. The canopy of teak trees is still open.

The 1948 and 1943 coupes have been subjected to fire and have little shrubby or herbaceous vegetation (Fig. 6). The teak canopy in the 1943 coupe is partially closed, and teak coppicing is heavy. The 1938 teak coupe has a heavy, closed canopy under which there is little vegetation; again the coppicing of teak is heavy. The 1933 coupe, a mixed plantation of native trees, was not studied. The 1928 coupe, a mixed plantation of native trees and teak trees, has a closed canopy and little ground vegetation. Sections of the 1920 teak coupe had undergone fire, leaving the ground free of vegetation. The shrub layer, however, is heavy in the unburned as well as the burned sections. The 1913 coupe is one of the original teak plant-

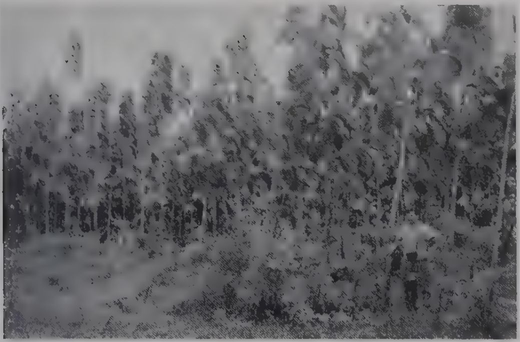

FIG. 3. The 1955 teak coupe at the Central Range Reserve, Brickfield Felling Series. Note dense growth of grass and other herbs in the open plantation.

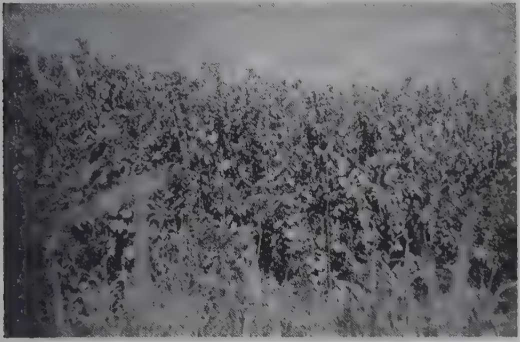

FIG. 4. The 1953 teak coupe at the Central Range Reserve, Brickfield Felling Series. The trees are 15-20 ft high, 4-6 in. in diameter. The canopy of the trees is partially closed.

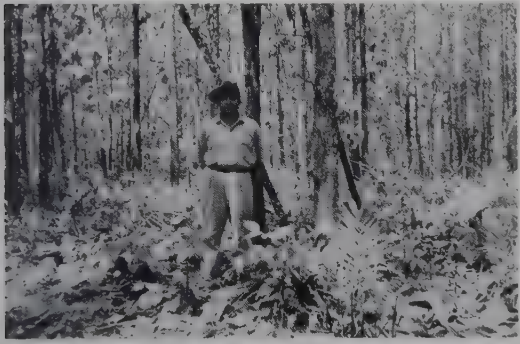

FIG. 5. The 1948 teak coupe at the Central Range Reserve, Brickfield Felling Series. The trees are 40-50 ft high and 6-10 in. in diameter. Note heavy leaf litter and young shrubs. The picture was taken in February after many of the teak trees had lost their leaves.

ings on the Island. The canopy is not closed because the area has been extensively thinned, and in the openings the ground cover is heavy. Teak coppicing is heavy in this coupe, and the crowns of teak trees are infested with the parasitic bird vines of the Loranthaceae.

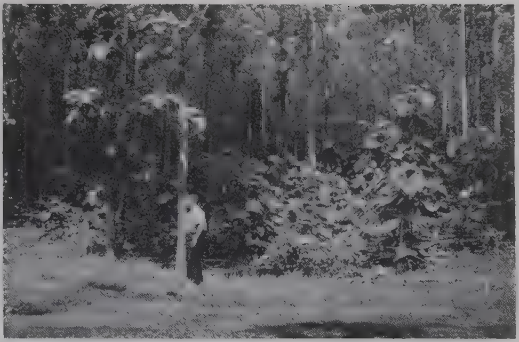

FIG. 6. The 1943 teak coupe in the Southern Watershed Reserve, Western Felling Series. The trees are 50 ft high and 10-12 in. in diameter. Note sparse condition of undergrowth and closed canopy.

In young plantations at the Western Felling Series light-demanding species of herbaceous plants are common. *Asclepias curassavica, Bidens pilosa, Lantana camera,* and *Solanum hirtum* were found only in the 1953 teak coupe. Grasses are common in the young plantations, and tend to remain through the 1948 coupe where the teak trees are beginning to form a partially closed canopy. *Paspalum rudgii, P. virgatum, Setaria poiretiana,* and *Stenotopharum secundatum* are abundant in both the 1953 and 1948 coupes. *Eugenia confusa, Bactris* spp., and *Desmoncus major* are common, widespread shrubs which were found in all the plantations studied. Many of the mature trees in the natural vegetation were also in the 1913 coupe. *Albizzia caribaea, Fagara trinitensis, Lonchocarpus sericeus,* and *Virola surinamenis* were common. These trees came in after the canopy had closed, and the environmental conditions of temperature, moisture, and light had returned approximately to the original conditions of the natural areas. In the natural vegetation there were a few species not observed in any of the teak coupes: *Chlorophora tinctoria, Hura crepitans, Sapium aucuparium,* and *Vitex divaricata.* Perhaps the change of conditions by the introduction of a deciduous tree species has affected the environment enough to keep these species from developing.

THE INFLUENCE OF FIRE ON THE DISTRIBUTION OF PLANTS

Teak plantations in Trinidad are plagued by fire each year during the dry season, February to May. At the beginning of this time the teak trees drop their leaves and these form a tinder dry layer 6-12 in. deep. Fires are started intentionally by the natives, accidentally by bottles which magnify the bright sunlight, or by smokers. Plantations bordered by major roadways are most susceptible to fires. The effect of fire on teak trees and on the distribution of vegetation was observed in both the 1949 coupe at Mount Harris and the 1920 coupe at Quarry Road.

Fires in the plantations are predominantly ground fires which spread quickly but are not sustained. Teak tree seedlings under one yr old are destroyed. Trees from one to 5 yrs are not killed outright, but fire stimulates growth of shoots on the lower portion of the trunk. These interfere with growth of the main stem often to such a degree that the plantation has to be cut over completely and re-established. In teak trees over 5 yrs the only effect of superficial ground fires is the stimulation of a few shoots near the base of the tree trunk, which do not interfere much with its growth. Although teak will withstand a quick ground fire, fire in debris piled against a trunk will quickly kill the tree.

The 1949 teak coupe at Mount Harris was burned during the 1956 and 1957 season. The coupe was observed in May, one month after a ground fire had consumed all the debris and much ground vegetation (Fig. 7). The development of ground vegetation was compared with the 1940 coupe not recently burned. In the burned coupe the bare ground had started to gully by erosion from the heavy rains. Living patches of shrubs such as *Bactris* spp., *Pentaclethra macroloba, Vismia cayennensis, Heliconia bihai,* and *Piper hispidum* had fire-blackened stems. Small plants of *Scleria arundinaceae, Pachystachys coccinea, Inga laurina, Heliconia hirsuta, Desmoncus major, Calathea lutea,* and *Brownea latifolia* were arising, many being shoots from old root stocks.

The 1940 coupe, on the other hand, had a dense undergrowth. In addition to the species listed above, the following were found: *Myrcia* spp., *Psychotria cuspidata, Warszewiczia coccinea, Heliconia* spp., *Flemingia strobilifera, Ischnosiphon arouma, Renealmia exaltata, Fagara martinicensis, Licania biglandulosa, Piper* spp., and *Pothomorphe peltata.* Shrubs were well established and tended to shade out the herbaceous vegetation. Seedlings of local trees were also becoming established in the understory.

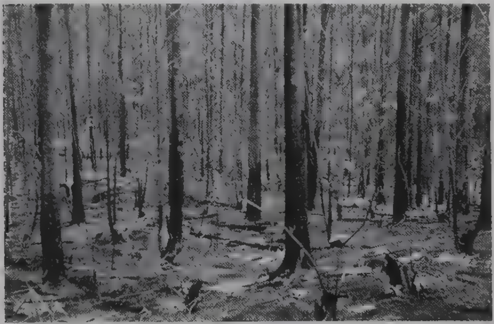

FIG. 7. The 1949 teak coupe in the Central Range Reserve, Mount Harris Felling Series. The trees are 25-30 ft high and 4-6 in. in diameter. The coupe has been burned the past 4 yrs and was burned 2 weeks before the picture was taken in February. Note lack of shrubs and herbs.

At Quarry Road, Southern Watershed Reserve, the 1920 teak coupe is divided by an asphalt roadway. One section, burned in February, 1958, was compared with the unburned section after one month. A few local trees larger than 4 in. in diameter were common to both sections. Trees that withstood fire included *Pisonia salicifolia, Platymiscium trinitatis, Cordia alliodora,* and *Fagara martinicensis.* Other species with large underground rhizomes which sent up new shoots were *Heliconia bihai* and *Maranta gibba.* Also evident were seedlings of fleshy seeded species, *Vismia falcata, Duggena hirsuta, Eugenia confusa, Desmoncus major,* and *Cassia fruticosa.*

Species in the unburned section of the coupe were similar to those in the natural areas. The following plants were not in the burned sections but were in the natural vegetation: *Andira inermis, Cedrela mexicana, Sabal* spp., *Bravaisia integerrima, Spondias mombin, Rudgea freemani, Tabebuia rufescens, T. serratifolia,* and *Hymenaea courbaril.* Shrubs were also common: *Miconia nervosa, Piper marginatum, Duggena hirsuta, Coccoloba latifolia.* In the burned area ground vegetation was sparse, with only a few species such as *Heliconia hirsuta, Calathea lutea,* and *C. trinitensis,* but the lianes *Paullinia pinnata, Doxantha unguis-cata,* and *Mucuna Sloanei* were common.

DISCUSSION

Brooks (1938) has proven that Trinidad teak is of high quality. He compared growth statistics of the trees in Trinidad with trees in the original habitat and rated Trinidad teak between class I and II of the Indian Nilembur plantation quality class scale. The effect of the establishment of this deciduous tree on natural vegetation has been drastic but temporary; this has been indicated by analysis of the natural vegetation and the vegetation which has successfully invaded the plantations.

The total number of species in each of the 3 study areas (Table V) increases from north to south. Conversely, the figures for annual rainfall decrease in the 3 areas from north to south. In the north at Mount Harris the heavy growth of canopy species, presumably a result of heavy rainfall, kept low the number of herbaceous plants. On the other hand, in areas of less rainfall and less overhead vegetation, many species of light-

TABLE V. Number of species in each coupe and per cent of total species

Teak Coupe	MOUNT HARRIS		BRICKFIELD		WESTERN FELLING SERIES	
	Total Species—66		Total Species—88		Total Species—103	
	Number of Species	Per cent of Total	Number of Species	Per cent of Total	Number of Species	Per cent of Total
Natural Vegetation........	33	50	50	57	34	33
1913..........					48	47
1920..........					42	41
1928..........					25	24
1938..........	32	48			10	10
1943..........	28	42	42	48	18	17
1948..........	1949—12	18	28	32	22	21
1953..........	1954—24	35	32	36	25	24

tolerant shrubs and herbaceous plants invaded the plantations.

Invasion of natural vegetation onto the teak land followed a clear pattern in the 3 areas; Table V gives the number of species in each 3 area. The young coupes show a higher percentage of species than the 10 yr old coupes, although the percentage figures rise in older coupes. At Mount Harris, the 1938 coupe recorded 48% for the number of species observed compared to a low of 18% in the 1944 coupe. At Brickfield the 1943 coupe registered 48% and the 1948 coupe registered a low of 32%. Quarry Road totaled 47% in the 1913 coupe, but in the 1938 coupe, a low of 10% was recorded. Because of the open nature of the vegetation at Quarry Road, grasses and more xeric vegetation remain under the teak for a longer period than in the other areas.

Plant species that first invade a newly established coupe are typically light-demanding. The Gramineae, Cyperaceae, and Solanaceae are well represented in the herbaceous undergrowth of young coupes. Their species tend to be short-lived because they are shaded by shrub species of Myrtaceae, Piperaceae, Rubiaceae, and Melastomaceae. These shrubs, along with species of Musaceae, Marantaceae, and Zingiberaceae, make the shade needed for development of tree species in the older coupes. Tree species are generally scarce in young plantations, but some coppice from root stalks, and a few other fast-growing ones can develop before they are shaded by other vegetation. Much of the vegetation under teak is fast-growing, bears seeds scattered by wind, or fruit eaten and dispersed by animals. Genera having species with seeds distributed by birds and bats are *Vismia, Didymopanax, Guazuma, Miconia, Byrsonima, Cercropia,* and *Psychotria.*

Tree species of the natural vegetation also develop under the shade of dense shrubs. Tree species found as seedlings in the undergrowth of the older coupes are the most common in the local natural forest. These species have efficient means of dispersal. At Mount Harris, *Carapa guianensis, Eschweilera subglandulosa,* and *Pentaclethra macroloba* are commonly found in the older coupes as well as in the natural vegetation. The plantations, where rainfall is lower, are not old enough at Brickfield for the development of many of the local climax tree species. *Sabal* spp., *Fagara* spp., and *Inga* spp. are present in the old plantations in this area. *Trichilia trinitensis, Bravaisia integerrima, Sabal* spp., and *Machaerium robinifolium* are climax species commonly found at Quarry Road in both the older plantations, the 1913 and 1920 coupes, and in the natural vegetation.

Successional development of vegetation underneath teak trees is similar to development of secondary vegetation in Trinidad (Greig-Smith 1952). Rapidity of development depends to a great extent upon the amount of rainfall. Invasion of primary trees of local natural vegetation at Mount Harris, which has the heaviest rainfall, is more rapid than at Brickfield. This in turn is more rapid than at Quarry Road, which receives the smallest amount of rain per year. The 1943 coupe at Mount Harris contains in its undergrowth many tree species found in the natural vegetation while the 1943 coupe at Brickfield has very few. At Quarry Road the primary species of the natural vegetation were established only in the older plantations, the 1913 and 1920 coupes.

Kenoyer (1929) found a similar development of secondary vegetation in old clearings on Barro Colorado Island (Panama). There grasses and sedges appeared first, along with abundant species of Solanaceae, Compositae, Amaranthaceae, etc. After the short-lived species died out, large-leaved monocotyledons, such as heliconias, and tree seedlings of *Trema, Cecropia, Apeiba,* and *Cordia* predominated. The secondary forest has persisted for 15 yrs with species of *Ficus, Inga, Protium* and many species of small melastomaceous trees and shrubs.

Development of vegetation in a teak plantation in Trinidad follows the general development of secondary forests in the tropics (Richards 1952). In time, the vegetation in the teak plantations comes to closely resemble in species content the natural vegetation of the surrounding area, mainly secondary forests.

Fires in teak plantations result in destruction of young teak trees and in the development on larger trees of shoots on the lower portion of the trunk. In older plantations a less obvious effect of fire is the destruction of soil humus and undergrowth vegetation. Without cover the open soil is exposed to heavy rain during the season when teak trees are leafless. Erosion and leaching of nutrients reduce the soil to a sterile condition. The effect of the erosion is not immediately obvious but in future years a decreased growth rate of the teak will result.

Invading plants in Trinidad teak coupes are similar to van Steenis's nomads in Malaya (van Steenis 1958a). These species maintain themselves at rain forest borders, are intolerant of shades, require high temperature for germination, have a profusion of flowers and seeds, efficient seed dispersal, sucker or coppice freely, and have a wide tolerance of soil and climatic conditions. The invading plants belong to a small group of families: Urticaceae, Moraceae, Graminae, Verbenaceae, Euphorbiaceae, Leguminosae, and Umaceae.

Large trees and shrubs are usually resistant to quick ground fires that plague older plantations. Vegetation having an underground rhizome sends up new shoots when the shoots are destroyed by fire. Some palm seeds are aided in germination by ground fires. Fleshy-seeded shrubs are among the first invaders of the burned teak plantations. Herbaceous vegetation does not soon invade because light needed for survival is cut off by the closed canopy.

SUMMARY

The establishment of teak plantations in Trinidad is a major project of the Forestry Department. Teak thrives best on well-drained soil and in a moist, warm tropical climate—conditions which are found throughout the island. The plants that invade the plantations and their succession were studied in relation to the environmental factors.

Three plantations studied, Mount Harris, Brickfield, and the Western Felling Series, are in a broadleaf evergreen forest: the first 2 in a *Carapa guianensis* and *Eschweilera subglandulosa* association, the third in a drier *Trichilia smithii* and *Brosimum alicastrum* association.

More species, many light-demanding, were found in the plantations with least rainfall, Western Felling Series. Plant invasion of the plantations follows a typical pattern in the 3 areas. Light-demanding species of Graminae, Cyperaceae, and Solanaceae invade newly established plantations. These plants are shaded by shrubs of the Myrtaceae, Piperaceae, Rubiaceae, and Melastomaceae. Tree species from the natural vegetation develop in older plantations under the shrubs. The plant succession is interrupted in many plantations by fire which destroys teak trees in young plantations and the undergrowth in older plantations exposing the soil to erosion.

REFERENCES

Bain, F. M. 1934. The rainfall of trinidad. Govt. Printing Office, Trinidad, B.W.I.

Beard, J. S. 1946. The Natural Vegetation of Trinidad. Oxford For. Mem. No. **20.**

Braun-Blanquet, J. 1932. Plant sociology: the study of plant communities. McGraw-Hill Book Co., New York.

Brooks, R. L. 1941. Notes on pure teak plantations in Trinidad. Caribbean Forester **3:** 25-28.

Chenery, E. M. 1952. The soils of Central Trinidad. Govt. Printing Office, Trinidad, B.W.I.

Greig-Smith, P. 1952. Ecological observations on a degraded and secondary forest in Trinidad, B.W.I. J. Ecology **40:** 283-330.

Hardy, F. 1956. Soils of Trinidad. Their genesis and main features. Unpubl. Pamph. ICTA Library, Trinidad, B.W.I.

Kenoyer, L. A. 1929. General and successional ecology of the Lower Tropical Rain Forest at Barro Colorado Island, Panama. Ecology **10:** 201-222.

Marshall, R. C. 1939. Silviculture of the Trees of Trinidad and Tobago, B.W.I. Oxford Univ. Press, London.

Richards, P. W. 1939. Ecological Studies on the rain forest of Southern Nigeria. J. Ecol. **27:** 1-61.

———. 1952. The tropical rain forest. Cambridge Univ. Press, London.

Ross, P. 1959. Teak in Trinidad. Economic Bot. **13:** 30-40.

Steenis, C. G. J. van. 1958a. Rejuvenation as a factor for judging the status of vegetation types: The biological nomad theory. Studies of Tropical Vegetation, UNESCO. 212-218.

———. 1958b. Basic principles of rain forest sociology. Studies of Tropical Vegetation, UNESCO. 159-165.

Weheking, L. and G. W. Smith. 1953. Trinidad rainfall, 1933-1952 and rainfall reliability in Trinidad. Govt. Printing Office, Port-of-Spain, Trinidad, B.W.I.

Williams, R. O., et al. 1928. Flora of Trinidad and Tobago. (Incomplete) Port-of-Spain, Trinidad, B.W.I.

REPORTS

RELATIVE POPULATIONS OF SMALL MAMMALS IN THREE FOREST TYPES OF NORTHEASTERN CALIFORNIA

STURGIS MCKEEVER
Department of Zoology, University of California, Davis[1]

For many years small mammals have been a hindrance to reforestation in several regions of western United States. Knowledge of the abundance of mammals in various habitats at different seasons is necessary for proper evaluation of their effect on their environment and for planning control measures.

In studies on the biology of small forest mammals, relative populations of various species in 3 types of coniferous forest were determined from January through December, 1958. The studies were made on 4 areas lying between 4,800 and 6,800 ft elevation in the region east of the crest of the Cascades in Lassen County, California. The forest types were: ponderosa pine (*Pnus ponderosa*), lodgepole pine (*Pinus contorta*), and mixed red and white fir (*Abies magnifica* and *A. concolor*). Populations of the various species of forest mammals undoubtedly vary from year to year, depending upon weather conditions, availability of food, and cyclic phenomena. Availability of food may vary for different forest types in a given year, but other changes probably are similar in various types within a limited region.

METHODS

Studies were made on 4 areas, two in ponderosa pine, and lodgepole pine and fir represented by one area each. A census of small mammals was made at least once a month in each of the 3 types. Snap traps were set in a line with trap stations at 50-foot intervals. A line consisted of 60 stations with both a rat and a mouse trap at each station, and 40 stations with only a mouse trap. The trap lines were placed in a different locality each month, but an attempt was made to place them in areas with similar topography and density of plant cover. All lines were maintained for 3 days and nights and checked each morning. Bait for rat traps was walnut kernels; bait for mouse traps was rolled oats and peanut butter.

Percent trap success for a given species was computed by dividing 100 times the number of individuals captured during a 3 day period by the number of trap nights for the same period. The number of trap nights was based upon rat traps only for chipmunks and larger forms, and on mouse traps only for mice and shrews. Percent trap success is here used as a measure of relative abundance. During the study, 754 mammals were collected in 15,497 trap nights.

Disadvantages and inaccuracies of the census method are realized. However, a review of recent literature, for example, Stickel (1946) and Sealander and James (1958), will show that a method which will give a really accurate estimate of the population of a single species of small mammal has yet to be devised. In effect, only a relative measure of the population is obtained, whatever the census method. Various species respond differently to a given trapping method, but for purposes of this study, the response of a given species was assumed to be similar in the different forest types.

DESCRIPTION OF HABITATS

Area 1 lies along Highway 36 immediately west of Willard Creek. Ponderosa pine was the dominant tree species; associates were white fir and Douglas fir (*Pseudo-*

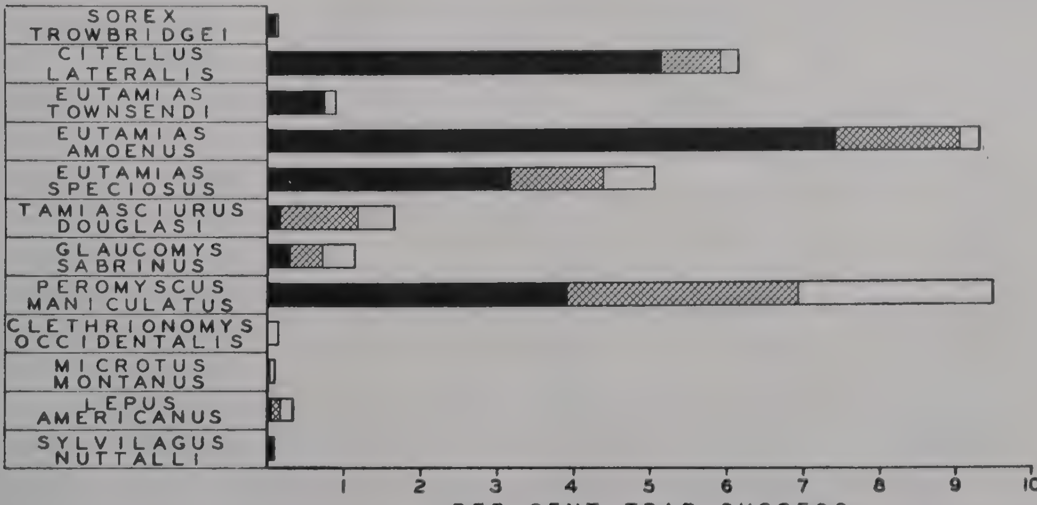

FIG. 1. Annual percentage catch of small mammals in 3 forest types of northeastern California for 1958. Figures for *Citellus lateralis* and *Eutamias* spp. are based upon data for May to December. Forest types are represented as follows: ponderosa pine, black bars; lodgepole pine, cross hatched; red and white fir, open bars.

---

[1] In cooperation with the Pacific Southwest Forest and Range Experiment Station, U. S. Forest Service, Berkeley.

tsuga menziesii) on north slopes, and incense cedar (*Libocedrus decurrens*) and juniper (*Juniperus californica*) on south slopes. Dominant trees were 12-30 in. dbh. Crown closure varied from 25-75% but was over 50% for most portions of the area. Young pines and firs up to 40 ft high have filled openings which were created when some trees were cut many years ago. Snow cover ranged from 2-4 ft deep from January to early April; the snow melted by May. This area was not trapped after May.

Area 2 consisted of selected blocks of the Black's Mt. Experimental Forest. Pondersosa pine was the predominant species; Jeffrey pine (*Pinus jeffreyi*), incense cedar and white fir constituted less than 20% of the stand. Dominant trees ranged from 12-48 in. dbh. Crown closure varied from 15-75%, but averaged less than 40% because many trees had been killed by insects. The understory was patchy; on some parts of the area there was no understory, on other parts it was very dense. Manzanita (*Arctostaphylos patula*), squaw mat (*Ceanothus prostratus*) and mules ear (*Wyethia mollis*) formed a medium to dense ground cover. The area receives up to 4 ft of snow, but there was no snow cover from June through December.

Area 3 lies at the base of Swain Mt. Lodgepole pine was the predominant tree species, but scattered ponderosa pine and white fir were present on some portions of the area. Dominant trees were 6-24 in. dbh. Crown closure ranged from 20-90%, and averaged approximately 60%. Manzanita, squaw mat, mules ear, and rabbit brush (*Chrysothammus* spp.) were abundant in openings. Snow cover was 2-5 ft deep from January through May; a 2-inch snow fell in November.

Area 4 was located on Swain Mt. and was covered with a dense, virgin stand of red and white fir. Dominant trees were 24-50 in. dbh and up to 150 ft tall. Crown closure was approximately 75%. Small openings, created by death of mature trees, were covered with a dense growth of young firs. Ground cover was very sparse and consisted of widely scattered herbs, grasses, dwarf manzanita (*Arctostaphylos nevadensis*), and chinquapin (*Castanopsis sempervirens*). Snow cover varied from 2-10 ft deep from January to May and some drifts persisted

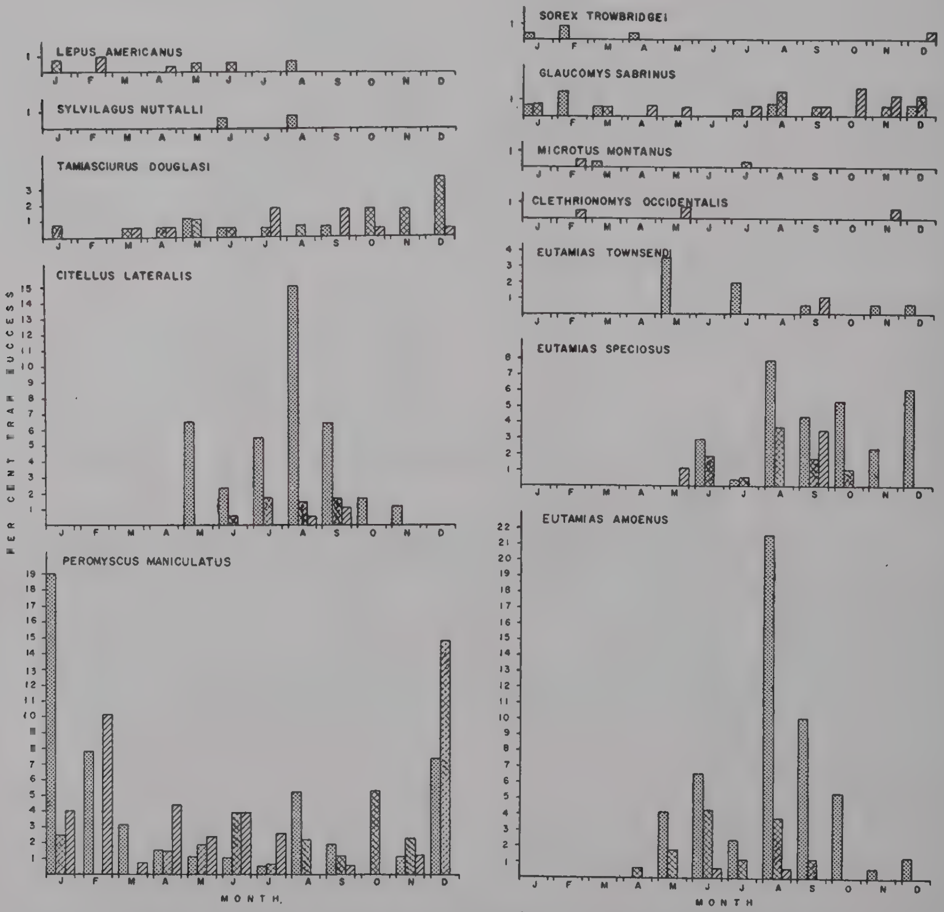

FIG. 2. Monthly percentage catch of small mammalodgepole pine, cross hatched bars; red and white fir, represented as follows: ponderosa pine, dotted bars; ls in 3 forest type of northeastern California. Types are diagonal lines.

Table I. Monthly catch of small mammals in three forest types of northeastern California

Forest type	Species	January	February	March	April	May	June	July	August	September	October	November	December	Total
Ponderosa pine	*Sorex trowbridgei*	1	2	—	1	—	—	—	—	—	—	—	—	4
	Citellus lateralis	—	—	—	—	11	4	14	21	10	3	2	—	65
	Eutamias townsendi	—	—	—	—	6	—	5	—	1	—	1	1	14
	Eutamias amoenus	—	—	—	—	7	11	6	30	16	9	1	2	82
	Eutamias speciosus	—	—	—	—	—	5	1	11	7	9	4	10	47
	Tamiasciurus douglasi	—	—	—	—	2	1	—	—	1	—	—	—	4
	Glaucomys sabrinus	1	2	1	—	—	—	1	1	—	—	—	1	7
	Peromyscus maniculatus	50	19	9	4	3	3	3	12	3	—	2	12	120
	Microtus montanus	—	—	1	—	—	—	—	—	—	—	—	—	1
	Lepus americanus	—	—	—	—	—	—	—	1	—	—	—	—	1
	Syluilagus nuttalli	—	—	—	—	—	1	—	1	—	—	—	—	2
Lodgepole pine	*Citellus lateralis*	—	—	—	—	—	1	3	2	3	—	—	—	9
	Eutamias amoenus	—	—	—	1	3	7	2	5	2	—	—	—	20
	Eutamias speciosus	—	—	—	—	—	3	1	5	3	2	—	—	14
	Tamiasciurus douglasi	1	—	1	1	2	1	1	1	—	3	3	6	20
	Glaucomys sabrinus	1	—	1	—	—	—	—	2	1	—	1	2	8
	Peromyscus maniculatus	7	—	—	4	5	10	1	3	2	9	4	24	69
	Lepus americanus	1	—	—	—	1	1	—	—	—	—	—	—	3
Red and white fir	*Sorex trowbridgei*	—	—	—	—	—	—	—	—	—	—	—	1	1
	Citellus lateralis	—	—	—	—	—	—	—	1	2	—	—	—	3
	Eutamias townsendi	—	—	—	—	—	—	—	—	2	—	—	—	2
	Eutamias amoenus	—	—	—	—	—	1	—	1	—	—	—	—	2
	Eutamias speciosus	—	—	—	—	2	—	—	—	6	—	—	—	8
	Tamiasciurus douglasi	—	—	1	1	—	—	3	—	3	1	—	1	10
	Glaucomys sabrinus	—	—	—	1	1	—	1	—	1	3	2	—	9
	Peromyscus maniculatus	11	21	2	12	7	9	7	—	1	—	2	—	72
	Clethrionomys occidentalis	—	1	—	—	2	—	—	—	—	—	1	—	4
	Microtus montanus	—	1	—	—	—	—	1	—	—	—	—	—	2
	Lepus americanus	—	2	—	1	—	—	—	—	—	—	—	—	3

until June. A 3-inch snow fell in November but melted within a week.

Results and Discussion

Percent trap success for the various species in the 3 forest types is presented for the entire study period in Figure 1, and for each month of the study period in Figure 2; the actual number of captures is presented in Table I. In Fig. 1, percent trap success for *Citellus lateralis* and *Eutamias* spp. was based upon the number of trap nights for the period when these animals were active. The following species were captured only sporadically: *Sorex trowbridgei, Clethrionomys occidentalis, Microtus montanus, Sylvilagus nuttalli,* and *Lepus americanus.* It is believed that the low percentage catch was a reflection of low populations of all these species except *Lepus americanus;* tracks of these animals indicated that they were more abundant in both the lodgepole pine and fir types than was demonstrated by trapping. For *Citellus lateralis, Eutamias amoenus, E. speciosus,* and *Peromyscus maniculatus,* monthly samples were considered to be sufficiently large to demonstrate basic seasonal fluctuations in the population, as shown in Fig. 2.

Of the 7 predominant species, *Peromyscus maniculatus* was most abundant. Populations were highest in ponderosa pine stands. The density declined during the summer months, but showed an increase in December in both ponderosa pine and lodgepole pine types. Tree seed was fairly abundant in both these types during the fall months. In contrast, fir produced practically no seed and very few mice were caught in the fir type during the fall. Fir seed was abundant during the fall of 1957, and mice were fairly abundant in the fir type during the early months of 1958.

Citellus lateralis and *Eutamias* spp. emerged from hibernation in late March on Area 1, and in early April on the other areas. Heavy snows fell throughout the region from April 2 to April 4 and probably delayed emergence on Areas 2, 3, and 4. Time of hibernation varied with the species. Almost all *Eutamias amoenus* and *Citellus lateralis* had disappeared by November; but many *E. speciosus* remained active until mid-December, even at 6,500 ft. A lasting snow cover did not fall until the last week of December, and the weather remained mild throughout the fall. Late hibernation probably was a reflection of the mild fall weather.

Young of *Eutamias amoenus, E. speciosus* and *Citellus lateralis* became active in early August, as shown by the marked increase in the population of these species at that time. Only one sub-adult, a *Eutamias amoenus,* was trapped in July. At Lake Almanor, Tevis (1955) found that young *Citellus lateralis* became active in early July.

Eutamias amoenus, E. speciosus and *Citellus lateralis* were most abundant in open ponderosa pine stands. Data used for comparing populations in the 3 forest types was obtained from areas which had not been cut or had only a few scattered trees removed many years ago. However, some trap lines were placed in cut-over areas, and data from these lines indicate that *Citellus lateralis* populations were approximately one-third higher in areas which had been cut during the last 3 years than in uncut areas. Three *Citellus* were caught in the fir type in the fall and were believed to have wandered there from adjacent pine stands at the base of the mountain. *Eutamias townsendi* was not abundant in any type, but showed some preference for dense stands containing some white fir.

Tamiasciurus douglasi and *Glaucomys sabrinus* could not be considered abundant in any of the 3 forest types. However, *Tamiasciurus* occurred most frequently in lodgepole pine and its population increased some in this type during the fall. The increase may have resulted from movement of the animals from the adjacent fir forest where the seed crop was a failure. Populations of *Glaucomys sabrinus* were approximately the same in each of the forest types.

SUMMARY

From January through December, 1958, small mammal populations were studied in 3 forest types in northeastern California, and the relative abundance of 12 species was computed. Five species were caught only sporadically. Predominant species were: *Peromyscus maniculatus, Citellus lateralis, Eutamias speciosus, E. amoenus, E. townsendi, Tamiasciurus douglasi* and *Glaucomys sabrinus. Peromyscus maniculatus, Eutamias* spp., and *Citellus lateralis* were most abundant in open stands of ponderosa pine. *Tamiasciurus douglasi* was most abundant in lodgepole pine. *Glaucomys sabrinus* populations were approximately the same in each of the 3 forest types.

REFERENCES

Sealander, John A. and Douglas James. 1958. Relative efficiency of different small mammal traps. Jour. Mamm. **39**: 215-223.

Stickel, Lucille F. 1946. Experimental analyses of methods for measuring small mammal populations. Jour. Wildlife Mngt. **10**: 150-159.

Tevis, Lloyd, Jr. 1955. Observations on chipmunks and mantled squirrels in northeastern California. Amer. Midl. Nat. **53**: 71-78.

A PORTABLE VISUAL PHOTOMETER FOR THE MEASUREMENT OF VERY LOW LIGHT INTENSITIES

DAVID GORDON EVANS[1]

An interpretation of mosquito behavior in the period from sunset to sunrise requires the measurement of light intensities far beyond the limits of ordinary light meters. Nielsen and Haeger (1955) obtained an approximation of such illuminations through a series of paired colored threads which could be distinguished by an observer in a stepped sequence of light intensities. For a more precise measurement of light levels during this behavioral period, a small visual photometer has been developed at this laboratory. This instrument makes possible the measurement of illuminations from 2000 lux to below 0.001 lux (from shaded sunlight to shaded starlight).

The light intensity is determined with a photometer by the comparison and matching of the unknown with a known illumination. In the photometer to be described this matching is accomplished on a divided white disk. Half the surface is opaque to reflect the light being measured and half is translucent for illumination from beneath by a calibrated source. The observer adjusts the brightness of the translucent sector by varying the voltage across its illuminating lamp until the illumination of the transmitted and the reflected areas appear equal. Each matched light intensity corresponds to a specific lamp voltage and thus it is conveniently indicated by a meter.

The prototype of our instrument is that described by Thomson (1940). In this prototype the matching illumination of known intensity is secured by a circular optical wedge which attenuates the light from a small electric bulb operating at a set voltage. By calibrating our photometer for different voltages across the lamp we have eliminated the need for the wedge. Thus the design and the construction have both been simplified.

This photometer is essentially of two sections: (1) A variable illuminator for the translucent portion of the disk consisting of the bulb, battery, and a variable resistance. (2) A multi-range voltmeter connected across the bulb. This circuit comprises the series of fixed resistors, a 7-point rotary switch and a 0 to 1.0 milliammeter (Figure 1).

The photometer disk is made from white filing card stock, half of it being saturated with paraffin wax to make it translucent (Figure 2).

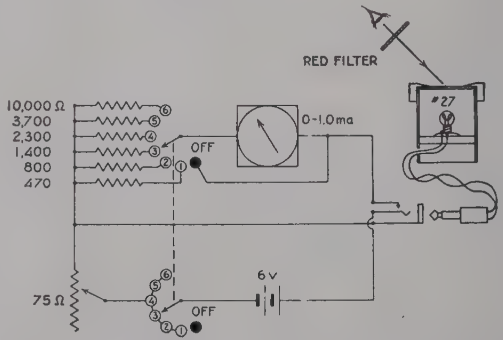

FIG. 1. Circuit diagram of the Photometer. For the protection of the meter the output jack is wired to open the battery circuit when the lamp is disconnected.

In use, the voltage across the illuminating bulb is adjusted through the rheostat until the line which separates the reflecting and the transmitting halves of the disk disappears. At this setting the lowest meter range which can be used is selected and the reading is made.

In the "off" position the range switch damps the meter. The other switch positions provide for the following full-scale readings: (1) battery voltage, (2) 2300 lux, (3) 230 lux, (4) 23 lux, (5a) 2.3 lux, (5b) 0.7 lux, and (6) 0.1 lux. "Full-scale" is actually about 95% of the scale for it is necessary to seek-out the best match of the light intensities from a little below and a little above the correct voltage.

For illumination greater than 0.6 lux (ranges 2 through

---

[1] Contribution No. 96, Entomological Research Center, Florida State Board of Health, aided by grant No. E-1408, National Institutes of Health, U. S. Public Health Service.

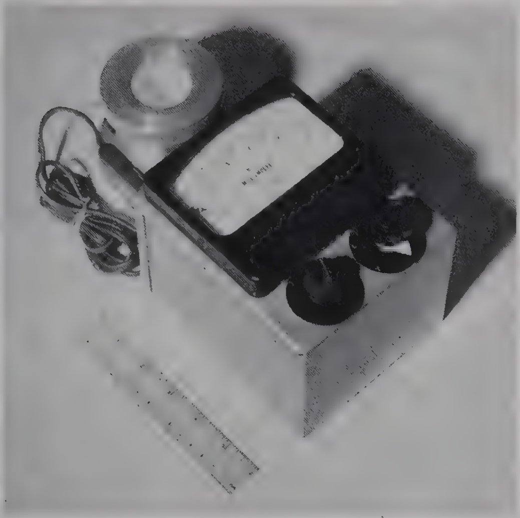

FIG. 2. The Photometer.

5a) the photometer disk is viewed through a dark red wratten filter #25 (A). This minimizes the color differences on the photometer disk between the light reflected and the light transmitted. Below 0.6 lux (ranges 5b and 6) the color differences are unimportant. (The 5th switch position is calibrated to be read with the red filter (5a) and without the filter (5b)).

Between 35° and 65° the vertical angle at which the photometer disk is viewed is not critical providing the observer does not shade the disk.

For the calibration of the photometer we set up an extended optical bench along which we obtained known luminous intensities from a U. S. Bureau of Standards calibrated electric lamp. The calibration curve given in Figure 3 is a sample only; each instrument should be individually calibrated.

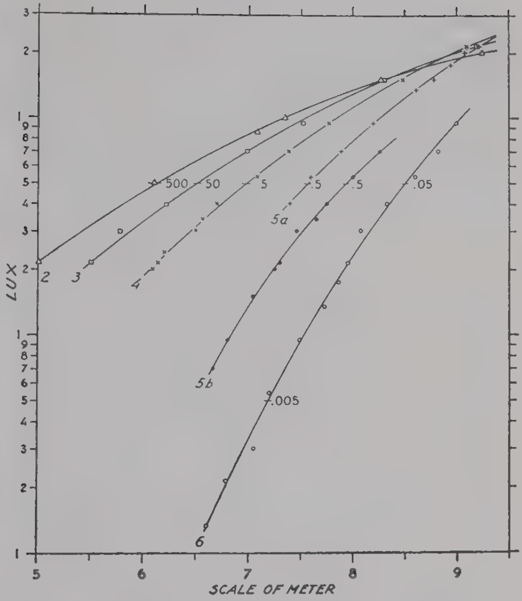

FIG. 3. Sample calibration curves for a Photometer.

Readings within the lower ranges of the photometer require good visual acuity and an accommodation of the observer's eyes to the low light levels being measured.

REFERENCES

Nielsen, Erik Tetens and James S. Haeger. 1955. A simple method for estimating low light intensities. Ecology **36:** 525-526.

Thomson, R. C. Muirhead. 1940. Studies on the behavior of *Anopheles minimus*. Part. I. Jour. Malaria Inst. India 3(2 + 3): 265-294.

DENSITY DEPENDENCE IN THE AUSTRALIAN THRIPS

FREDERICK E. SMITH
Zoology Department, University of Michigan, Ann Arbor

The study of *Thrips imaginis* by Davidson and Andrewartha (1948a, b) has been cited as an example of an animal population whose numbers are controlled by the weather. To quote from Andrewartha and Birch (1954): ". . . not only did we fail to find a 'density-dependent factor,' but we also showed that there was no room for one." A search for density-dependence in these data has never been published.

It is the purpose of this note to show that such a search supports the thesis of strong density-dependence in this population, and furthermore that the analytic model used by Davidson and Andrewartha is not appropriate to their theoretical interpretation, and is in fact appropriate to the concept of density-dependent regulation.

Density-dependence exists when population change depends upon population size. Usually an inverse relation is expected; when the population level is high, decreases tend to occur, and vice versa. Responses to other factors are not ruled out; changes in the weather, for example, can certainly influence population change. In a density-independent system, population changes are largely explained in such a way, with population size exerting no effect upon population change, while in the density-dependent system population size persists as a powerful factor acting together with other factors.

A search for density-dependence involves an analysis of population changes, which in turn require accurate censuses of population size. The data in the thrips study are among the most detailed and comprehensive that are published for a field population. Population estimates were made almost daily during the periods of observation, producing monthly means with very small sampling errors. Such means are published by Davidson and Andrewartha for 81 consecutive months (1948a) and during the late spring and early summer for 14 years (1948b).

Seasonal trends are similar from year to year (Figure 1), showing population lows in winter and again in late summer, with moderate rises in the autumn and sharp rises to annual maxima in the spring. Davidson and Andrewartha treated years as a form of replication, thus permitting analyses of population size at certain times of the year in terms of weather factors for those years. The same approach is used here to permit an analysis of population change.

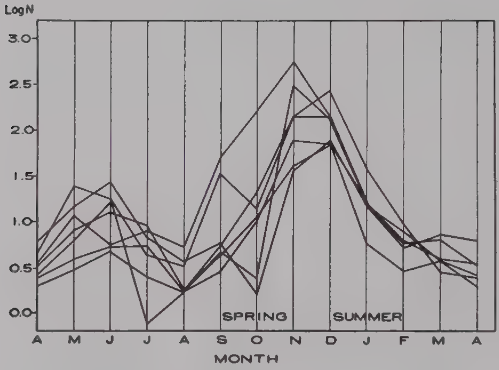

FIG. 1. The logarithm of the average population size per month for 81 consecutive months in the study of *Thrips imaginis* by Davidson and Andrewartha (1948a). The identity of curves through common points, which is of no importance in this paper, can be accomplished by reference to the original work.

Davidson and Andrewartha converted census data to logarithms, since rates of change are best expressed in this way. As stated by them (1948b): "Experience indicates that the thrips numbers are not likely to change by a constant quantity for each increment of the causal agent, but rather are they likely to change by a constant proportion." Happily, this transformation produced frequency distributions very close to normal distributions, and produced sampling errors that were independent of population size. Thus, the data become ideally suited to statistical analysis.

Averages of the logarithms of population size for 3 calendar periods are published for 14 years (y's are the symbols used in the original papers; notations at the right will be used in this paper):

y_4 = average log N for the period 1-31 October = $\overline{\text{16 Oct}}$
y'_6 = average log N for 17 Oct. to 15 Nov. = $\overline{\text{1 Nov}}$
y_5 = average log N for the period 1-30 November = $\overline{\text{16 Nov}}$

Each of these averages covers a period of about 30 days, and is based on censuses from as few as 22 to as many as 27 days, the missing days being mostly Sundays and holidays. Unpublished data exist for September and December which were utilized in other averages discussed below.

Estimates of the rate of population change can be obtained by differences from these average logarithms. Three such differences will be used here:

$y_5 - y_4$ = ave. 1-30 Nov. minus ave. 1-31 Oct. = Δ log N 16 Oct. to 16 Nov.
$y'_6 - y_4$ = ave. 1-15 Nov. minus ave. 1-16 Oct. = Δ log N 8 Oct. to 8 Nov.
$y_5 - y'_6$ = ave. 16-30 Nov. minus ave. 17-31 Oct. = Δ log N 23 Oct. to 23 Nov.

Note that in the last 2 the effect of subtraction is such that the period of overlap in the two 30-day means (17-31 Oct. in the second difference, 1-15 Nov. in the third) is virtually subtracted from itself and hence disappears. Thus all 3 differences span a period of about one month.

The correlations of these differences with appropriate estimates of population size (at or near the beginning of the period covered by the difference) are given on Table I. The consistency with which a negative correlation emerges is such that density-dependence is strongly suggested.

TABLE I. Correlations of population change (Δ log N) with population size (log N) using 14 years of data from Davidson and Andrewartha (1948b)

△ log N	log N	r	P
16 Oct. to 16 Nov.......	$\overline{\text{16 Oct.}}$	−0.80	<.001
8 Oct. to 8 Nov.......	$\overline{\text{16 Oct.}}$	−0.60	.03
23 Oct. to 23 Nov.......	$\overline{\text{16 Oct.}}$	−0.81	<.001
23 Oct. to 23 Nov.......	$\overline{\text{1 Nov.}}$	−0.73	.004

Davidson and Andrewartha criticized the use of calendar periods as a basis for comparing different years on the grounds that spring arrives at different times in different years. They attempted to coordinate the seasons by using the time of the summer maximum of the population as a reference point. This time varied between 15 November and 13 December. After shifting each year's data to the left or right until the times of the maxima coincided, they computed new averages. Three such averages are published:

y_1 = ave. log N from 7 days before to 7 days after the maximum = $\overline{7-7}$
y_2 = same for the period 30-1 days before the maximum = $\overline{30-1}$
y_3 = same for the period 60-1 days before the maximum.

The last average covers a very long period. Estimates for the average of the period from 60 to 31 days ($= \overline{60\text{-}31}$) before the maximum can be obtained, however, by subtracting y_2 from $2y_3$. The estimates are inaccurate only to the extent that the number of days averaged in y_3 is not exactly twice the number averaged in y_2.

Differences can be taken as estimates of population change:

$y_2 - (2y_3 - y_2)$ = ave. 30-1 days minus ave. 60-31 days = Δ log N −45 to −15
$y_1 - (2y_3 - y_2)$ = ave. 7-7 minus ave. 60-31 days = Δ log N −45 to 0
$y_1 - y_2$ = approx. ½(7-1 before) plus 0-7 after the maximum minus ave. 30-8 days before = Δ log N −19 to +1

The last difference is especially awkward since the overlapping means are based on unequal time periods. Such irregularities do not, however, introduce bias into the analysis.

Correlations based on these time-shifted data are given on Table II. Obviously, attempting to coordinate the seasons has had little effect upon the inverse relation between population change and population size. It now remains to be seen whether this relation will persist if extrinsic factors are brought into the analysis.

TABLE II. Similar to Table I, but with the daily estimates shifted in time each year so that the summer maxima coincide. Times refer to days before or after the maximum

△ log N	log N	r	P
−45 to −15..........	$\overline{60\text{-}31}$	−0.76	.002
−45 to 0..............	$\overline{60\text{-}31}$	−0.82	<.001
−19 to +1...........	$\overline{60\text{-}31}$	−0.57	.04
−19 to +1...........	$\overline{30\text{-}1}$	−0.49	.08

Of the several weather factors studied by Davidson and Andrewartha, 2 were the most consistently significant, and accounted for the majority of the relation they found between population size and weather. These were the effective degree-days between the first fall rain and the end of winter (x_2 in their paper), and the total inches of rain during September and October (x_3).

The correlations of the 6 estimates of population change with these 2 factors are given on Table III. For data based on calendar periods, a general conclusion that the 2 factors are relevant is acceptable, while for the data based on time-adjusted periods no significance is evident.

TABLE III. Correlations of population change with effective degree-days between the first fall rain and Aug. 31 (x_2), and with inches of rain during Sept. and Oct. (x_3)

△ log N	CORRELATION WITH x_2		CORRELATION WITH x_3	
	r	P	r	P
16 Oct. to 16 Nov.	−0.57	.04	0.54	.05
8 Oct. to 8 Nov.	−0.42	>.10	0.59	.03
23 Oct. to 23 Nov.	−0.58	.03	0.52	.06
−45 to −15.....	−0.29	>.10	0.35	>.10
−45 to 0........	−0.31	>.10	0.23	>.10
−19 to +1......	−0.22	>.10	−0.16	>.10

The 2 weather factors themselves are correlated —0.63, and each is more or less correlated with the various estimates of population size. With so many interrelations present, statistical procedures are needed for clarification. Davidson and Andrewartha used multiple regressions. Where the prediction of a quantity is desired through the simultaneous use of several possible predictors, such a technique is indicated. In this case, however, the relative roles of possible factors are to be compared. For this, the related process of partial correlation is indicated.

Two of the kinds of estimates of population change were chosen for this analysis: Δ log N 16 Oct. to 16 Nov., and Δ log N —45 to —15. Each of these spans one month, and is based on 30-day means. Moreover, they afford an interesting comparison, since the average date of the population maximum was Dec. 1. For each, 3 factors are considered simultaneously: the initial 30-day mean, winter degree-days, and spring rain. Two of these were partialled out in the process of computing the partial correlation of the third with population change. Thus, each partial correlation shows the degree to which population change is related to a given factor, excluding that which can be attributed to the other factors.

The results of this analysis are given on Table IV. Of major interest is the observation that the inverse relation of population change with population size remains strong, and is much stronger than relations of population change with either of the 2 weather factors.

TABLES IV. Partial correlations of population change (Δ log N) with population size (log N), winter degree days (x_2), and spring rain (x_3). In each case 2 of the 3 factors have been partialled out. In the first row, log N is for the average of the period 1-31 Oct.; in the second row it is for the average of the period 60-31 days before the summer population maximum

△ log N	log N	P	x_2	P	x_3	P
16 Oct. to 16 Nov......	−0.70	.02	0.36	>.10	0.27	>.10
−45 to −15..........	−0.84	<.001	0.63	.03	0.49	.11

A comparison of the 2 sets of partial correlations supports the attempt by Davidson and Andrewartha to coordinate seasons. Using time-shifted data (2nd row), the partial correlations of population change and each of the weather factors are reasonably high, suggesting that with proper time-adjustments these effects can be revealed. In spite of this, however, the inverse relation of population change and population size is extremely high.

Although the method of correlation analysis is a powerful technique for discovering density-dependence, it cannot be used where the sampling errors of population size are large relative to the amount of change occurring in population size. Davidson and Andrewartha (1948a) reported a relative standard error in the daily estimates of about 15%. In terms of logarithms and of averages of many days, this error becomes negligible. Thus, the inverse relations obtained above cannot be ascribed to sampling error. Where errors are large, however, another technique is needed.

A related approach that escapes the problem of sampling error utilizes an analysis of the variance of population size at different times. This approach has broad applications, especially where a series of life tables or other population histories are available. Density-dependent control of population size produces a given level of variation among various sub-populations at any given time. Should this control be relaxed, the sub-populations being in slightly varying environments will steadily diversify—that is, the variance will increase. Variance will decrease again if and when regulatory mechanisms again operate.

In a truly density-independent model, of course, there is no method of reducing variance, since this can occur only through a negative correlation of population change and population size.

The 81 consecutive monthly means of thrips per flower (Davidson and Andrewartha 1948a), converted to logarithms, are shown on Fig. 1. Using years as replications, variances for each month can be computed, having 6 degrees of freedom for 9 months, and 5 for the other 3.

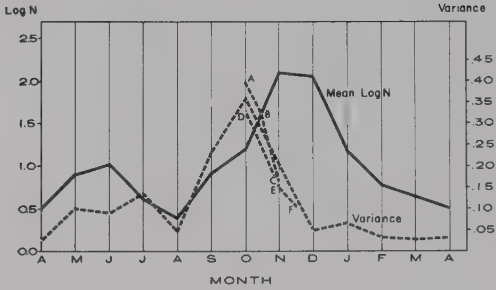

FIG. 2. The variance of the logarithm of the average population size each month, using the 6 and ¾ years of data as a form of replication. The average curve of population size from Fig. 1 is also shown. Additional points show the variance using 14 years of data from Davidson and Andrewartha (1948b).

These variances, together with an average curve of population size, are shown on Figure 2.

The most striking behavior of the variance is its sharp rise from August to October, during the early phase of spring growth, followed by an equally sharp decrease from October to December, during the later phase of spring growth and into the beginning of population decrease. These variations in the variance are much too large to be attributed to chance. Furthermore, using the 14-year data, the variances of the 3 calendar periods (points A, B, C) and of the 3 time-shifted periods (points D, E, F), which cover the later phase of spring growth, show similar decreases.

The low variance through 9 of the months indicates that the thrips population is regulated by density-dependence most of the time. It should be emphasized, moreover, that this cannot be achieved through minor effects. Where the standard deviations of population size and population change are s_a and s_b respectively, a correlation of at least $-\frac{1}{2}(s_a/s_b)$ is necessary to prevent an increase in population variance. Only in September and October, when a marked increase in flower densities occurs, does the variance of population size behave according to the requirements of a density-independent system.

Reconciling these analyses with those of Davidson and Andrewartha is possible if their model is examined. Where density-independent interpretations are to be made, it is the relation of environmental factors to rates of change in population size that must be studied. Furthermore, as suggested by Davidson and Andrewartha, it is the relative change (percentage change in size, also measured by the change in the logarithm of population size) that should be related quantitatively to environmental factors. Hence, the appropriate multiple regression is:

$$\Delta \log N = a + bx_1 + cx_2 + dx_3 + \ldots.$$

where the x's represent various measures of the weather.

Population size, or its logarithm, will show a much poorer relation to weather factors if the system is density-independent. For example, although a population may always double in one month under given environmental conditions (a density-independent hypothesis), the size may in one case be very small and in another be very large. In a density-independent system, the approach is such that only population change can be accurately predicted; size cannot be predicted at all unless a known size is used for one point in time, and later sizes predicted through the successive application of predicted rates of change.

Since Davidson and Andrewartha used population size rather than change in their model:

$$\log N = a + bx_1 + cx_2 + dx_3 + \ldots$$

and obtained high degrees of predictibility, they have in fact demonstrated regulation in a natural population. Their multiple regression implies a predicted population level for specific environmental conditions, and the actual population follows this predicted level with remarkable fidelity. The predicted levels must, therefore, represent some kind of equilibrium.

The weather factors used are related frankly by Davidson and Andrewartha to the abundance of flowers, which are not only the food but also the habitat of the thrips. It is not unbelievable, therefore, that such factors as winter degree-days and spring rain should powerfully influence the regulatory system of the thrips.

It is not the purpose of this note to identify the density-dependent mechanism. The evidence presented by Davidson and Andrewartha that food is not limiting is convincing. So is their argument that density levels (thrips per rose) correlate with flower density. It is evident that some one or more factors hold the thrips to very low levels in the flowers. Predation, parasitism, and other density-dependent mortalities are likely to interact with the capacity of the thrips to increase, which would be a function of flower density, so as to produce a variable equilibrium level. Predation and parasitism would also suffer time lags which could explain the sharpness of the peak of the annual maximum. Whatever factors control the abundance of thrips, it is evident that they have so far been overlooked.

Throughout this paper no distinction has been made between unadjusted (y) and adjusted (y′) means from the original papers. Adjusted means are corrected for "activity" through the use of a multiple regression with the momentary weather. Although this regression is significant, it accounts for only 10% of the variance of daily counts around the population trend. In the means this becomes a trivial correction, presumably because over a 15, 30, or 60 day period these corrections nullify each other. This is shown in the correlation coefficient of +0.997 between y_2 and y'_2, the only case where both adjusted and unadjusted figures were published. In Andrewartha and Birch (1954), pages 571 to 574 can be deleted without loss to the analysis.

SUMMARY

Direct analysis of the published data on the thrips population studied by Davidson and Andrewartha reveals a strong inverse correlation between population change and population size. A rapidly decreasing variance in population size is also shown to exist during the later portion of the spring population increase. Such evidence of density-dependence persists through the use of partial correlations using environmental factors known to be related to population size. The multiple regression model used by Davidson and Andrewartha is not appropriate for the interpretations they have made. They have in fact demonstrated the degree to which the population conforms to a predicted level, hence the degree to which the population is regulated. They have no evidence for a density-independent system. The regulatory system by which the

thrips are held to levels well below that set by their food supply remains unknown.

References

Andrewartha, H. G., and L. C. Birch. 1954. The Distribution and Abundance of Animals. Univ. Chicago Press.

Davidson, J. and H. G. Andrewartha. 1948a. Annual trends in a natural population of *Thrips imaginis* (Thysanoptera). J. Anim. Ecol. **17**: 193-199.

———. 1948b. The influence of rainfall, evaporation, and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). J. Anim. Ecol. **17**: 200-222.

THE FOOD HABITS OF RODENTS ON RANGELANDS OF SOUTHERN IDAHO

Donald R. Johnson
Forestry and Range Management Section, Colorado State University, Fort Collins, Colorado

The relationship of the population density of rodents to the degree of range use has received considerable attention in recent decades. Yet, the food habits of most rodents inhabiting western rangelands are not well known. A knowledge of both the population dynamics and the food habits is necessary before the relationship of rodents to rangelands can be accurately known.

A study of the food habits of rodents inhabiting the sagebrush and shadscale associations in southern Idaho was undertaken during 1957 in an effort to gain an understanding of the seasonal diets of rodents and their effect on forage palatable to livestock. The Raft River Valley in Cassia County was chosen as the principal area of study because ecological information was available from the area which was useful in designing the investigation.

The Raft River Valley has a history of heavy use by livestock beginning about 1870. During the early part of this century it was one of the principal sheep winter ranges in Idaho. Unsuccessful dry farming, drought, insect attacks, and overgrazing have depleted the original vegetation and promoted a serious invasion of halogeton (*Halogeton glomeratus*) (Tisdale and Zappetini 1953).

In addition to this principal area of study, supplementary investigations were conducted at an exclosure 6 miles southwest of Burley, Idaho. Other trapping was conducted on the Elmore Desert, Elmore County, and in the vicinity of Murphy Hot Springs, Owyhee County.

The author gratefully acknowledges the counsel and assistance of Earl J. Larrison, University of Idaho, the project leader in this study. He outlined the problem and conducted preliminary investigations. Drs. William H. Baker and William F. Barr, University of Idaho, and Robert H. Haas, Agricultural Research Service, Twin Falls, also rendered valuable assistance. The project was financed as part of the Special Research Program of the University of Idaho, Project SR-48.

Methods

Museum Special traps placed in transect lines of 50 traps each were used to collect rodents. Rolled oats was used as bait.

Stomach contents were prepared on slides using Hertwig's Solution (Baumgartner and Martin 1939) as a clearing agent and Apathy's Gum Syrup (Dusi 1949) as a mounting medium. Identification of the material found in the stomachs was made by comparing its microscopic characters with reference material. Slides of the stomach contents were made after each trapping without regard to sex or age of the rodents. Any bias existing in regard to sex or age is the result of differential effectiveness of the trapping technique. The contents of the cheek pouches were collected and identified.

An effort was made to trap in stands of vegetation which were homogeneous in composition. The following stands in the Raft River Valley, near Malta, were trapped during April, June, and August: big sagebrush (*Artemisia tridentata*), moderately grazed shadscale (*Artiplex confertifolia*), depleted shadscale, an area cleared of big sagebrush which supported a dense stand of peppergrass (*Lepidium perfoliatum*) and halogeton, and a seeded stand of crested wheatgrass (*Agropyron cristatum*). Most of the data presented were obtained from rodents trapped at these 5 sites. The rodents trapped at 11 other sites of varying composition provided supplementary information.

Results of Stomach Examinations

The deer mouse (*Peromyscus maniculatus*) was caught in sufficient numbers to permit the analysis of its food habits by month and by site (Table I). Deer mice relied heavily on arthropods for food during the period of the investigation. Lepidopterous larvae, carabid beetles, spi-

Table I. Frequency of food items found in the stomachs of 405 deer mice trapped in the Raft River Valley. Frequencies listed for sites are means of 3 months. Frequencies listed for months are means for 5 sites. Items with frequencies never exceeding 5% are not listed

Food Item	Site					Month		
	Big sagebrush	Shadscale	Depleted Shadscale	Peppergrass-Halogeton	Crested wheatgrass	April	June	August
Arthropods	80	95	90	83	89	78	95	90
Seeds								
Halogeton	41	24	0	58	20	58	19	0
Shadscale	4	29	28	0	0	27	2	0
Grass	0	0	0	2	23	0	0	19
Peppergrass	0	0	2	11	7	0	14	0
Prickly pear	7	14	16	10	4	0	0	34
Tansy mustard	4	2	7	1	1	0	8	1
Leaves								
Halogeton	34	22	7	21	12	39	8	2
Shadscale	5	14	26	0	0	3	10	14
Tansy mustard	12	2	6	4	0	11	5	0
Grass	3	10	9	13	77	17	34	25
Peppergrass	0	0	6	0	1	0	5	0
Russian thistle	0	0	0	14	4	0	2	12
Miscellaneous								
Mammalian hair	7	12	8	9	13	13	12	3
Prickly pear stems	5	9	1	2	1	0	1	9
Sample Size	76	58	88	91	92	157	130	118

ders, and weevils were the arthropods most frequently found in the stomachs of deer mice trapped in April and June (Table II).

The seeds of halogeton and shadscale were important foods in the diet of deer mice during April. Grass was taken throughout the spring and summer months, particularly in June. The increased use of the leaves of Russian thistle (*Salsola kali*) and the fleshy parts of prickly pear (*Opuntia* sp.) during August may indicate that deer mice were using these plants as a source of moisture.

Some small birds and mammals were used as food. Feathers, flesh, and hair were found in a number of stomachs. The frequency of hair found in stomachs is not an accurate indication of the use of mammals as food since some hair may be ingested while caring for the pelage.

TABLE II. Frequencies of certain arthropods found in the stomachs of 3 insectivorous rodents trapped at 5 sites in the Raft River Valley. Those arthropods with frequencies never exceeding 5% are not listed

Arthropod	SPECIES					
	Deer mouse		Least chipmunk		Western harvest mouse	
	April	June	April	June	April	June
Lepidopterous larvae	50	59	33	70	54	67
Carabid beetles	18	44	11	19	6	0
Spiders	17	15	44	9	9	8
Weevils	17	2	11	6	3	8
Scarabaeid beetles	0	20	0	2	0	0
Ants	0	5	11	0	0	0
Nitidulid beetles	0	2	0	13	0	0
All arthropods	78	95	83	75	64	87
SAMPLE SIZE	157	145	12	53	33	24

Least chipmunks (*Eutamias minimus*), western harvest mice (*Reithrodontomys megalotis*), Ord's kangaroo rats (*Dipodomys ordi*), and chisel-toothed kangaroo rats (*Dipodomys microps*) were trapped in sufficient numbers to permit the comparison of their food habits by season (Table III).

Least chipmunks were trapped in greatest numbers at the depleted shadscale site. In the stomachs examined, arthropods occurred in greater frequency than any other food. Lepidopterous larvae, spiders, carabid beetles, and weevils were the principal kinds taken (Table II). The seeds and fleshy parts of prickly pear were important constituents of the diet in August.

The western harvest mouse was trapped in greatest numbers in the stand of peppergrass and in the seeded stand of crested wheatgrass. The seeds and vegetative parts of crested wheatgrass were frequently eaten during August. Like the deer mouse and the least chipmunk, the western harvest mouse relied heavily on arthropods for food during the spring and summer months.

The Ord's kangaroo rat was frequently caught along roadsides where weedy plants provided food and cover. The loosened earth resulting from road construction may also have been a factor which promoted higher populations along roadsides. The Ord's kangaroo rat subsisted on diverse kinds of food during the spring and summer months. The seeds and leaves of several kinds of plants were eaten. Arthropods were infrequently taken (Table III).

The chisel-toothed kangaroo rat was most frequently trapped in the moderately grazed stand of shadscale. It relied heavily on the leaves of shadscale for food. In western Utah, Fautin (1946) found similar conditions. He reported that chisel-toothed kangaroo rats occurred in greatest numbers in stands of shadscale and that captive animals eagerly ate the leaves of shadscale.

TABLE III. Frequency of the food items found in the stomachs of 4 species of rodents trapped at various sites in the Raft River Valley. Items with frequencies never exceeding 5% are not listed

Food Item	SPECIES											
	Least Chipmunk			Western Harvest Mouse			Ord's Kangaroo Rat			Chisel-toothed Kangaroo Rat		
	April	June	August	April	June	August	April	June	August	April	June	August
ARTHROPODS	83	75	47	64	87	81	7	0	13	0	0	9
SEEDS												
Halogeton	25	4	0	76	62	0	100	48	16	22	5	0
Shadscale	58	15	0	6	0	0	3	0	13	0	7	4
Peppergrass	0	4	0	0	17	0	0	0	11	0	0	4
Prickly pear	0	0	63	0	0	3	0	0	16	0	0	8
Grass	0	9	16	0	0	41	0	0	5	0	0	2
Tansy mustard	0	9	0	0	0	7	0	61	16	0	53	36
LEAVES												
Sweet clover	0	0	0	0	0	5	0	0	8	0	0	0
Sagebrush	0	2	0	12	0	0	3	0	0	0	5	0
Grass	0	8	0	10	0	26	0	14	13	0	0	8
Halogeton	33	2	16	6	8	0	24	20	11	7	30	11
Shadscale	33	17	0	3	4	2	0	11	5	85	86	72
Russian thistle	0	4	0	0	0	13	0	20	11	0	0	0
Tansy mustard	0	0	0	0	0	0	3	20	0	0	30	6
Kochia	0	0	0	0	0	0	0	5	0	0	9	0
Salt sage	0	0	0	0	0	0	0	0	16	0	0	8
MISCELLANEOUS												
Prickly pear stems	0	0	32	0	0	0	0	0	0	0	0	0
Unidentified material	0	9	21	0	0	13	0	32	44	0	0	8
SAMPLE SIZE	12	53	19	33	24	19	29	44	38	27	43	33

The infrequent use of big sagebrush, bud sage (*Artemisia spinescens*), kochia (*Kochia americana*), sweet clover (*Melilotis alba*), and salt sage (*Atriplex nuttallii*) by these rodents was the result of preference, availability or a combination of these factors.

Six other species of rodents were infrequently trapped. Six Townsend's ground squirrels (*Spermophilus townsendi*) were found to have eaten the leaves of shadscale, halogeton, and budsage. Ten little pocket mice (*Perognathus longimembris*) consumed primarily shadscale seeds. The seeds of salt sage and grasses were the principal contents of the stomachs of 23 Great Basin pocket mice (*Perognathus parvus*). Six desert wood rats (*Neotoma lepida*) had eaten shadscale leaves and the fleshy parts of prickly pear. Seventeen northern grasshopper mice (*Onychomys leucogaster*) had eaten arthropods almost exclusively. Feathers were also found in some stomachs. The stomachs of 5 sagebrush voles (*Lagrus curtatus*) contained grass.

FOOD HABITS AT THE BURLEY EXCLOSURE

An area of 40 acres near Burley was fenced to exclude livestock in 1930. One half of the area within the exclosure was cleared of vegetation in order to study plant succession. The remainder supported a stand of big sagebrush (Piemeisel 1945).

At the time of investigation, August 1957, the cleared area within the exclosure supported a dense stand of grasses, principally downy chess (*Bromus tectorum*), and a few scattered big sagebrush plants. Outside the exclosure there was a dense stand of big sagebrush with few grasses present. The grassy area within the exclosure and an adjacent area outside it were trapped to secure rodents for comparison of the food habits.

Of the deer mice trapped within the exclosure, arthropods, grass, and downy chess seeds occurred in 96, 79, and 62% respectively of the 24 stomachs examined. Outside the exclosure, these same items occurred in 100, 50, and 20% respectively of the 30 stomachs examined. The marked reduction in the use of grass and grass seeds outside the exclosure probably results from decreased availability of these foods.

Ord's kangaroo rats, least chipmunks, Great Basin pocket mice, and western harvest mice were not caught in sufficient numbers on both areas to permit such a comparison. Downy chess seeds were an important part of the diet in these 4 species. Arthropods comprise a large part of the diet of least chipmunks and western harvest mice.

Results of Cheek Pouch Examinations

Table IV presents the frequency of certain food items found in the cheek pouches of 3 kinds of heteromyid rodents trapped in three localities in southern Idaho. The material carried in the cheek pouches was usually the same as that found in the stomachs.

Table IV. Frequency of food items found in the cheek pouches of 3 kinds of heteromyid rodents trapped in 3 localities. Frequencies listed for the Raft River Valley are means of 3 months. Frequencies listed for the Elmore Desert and Murphy Hot Springs are for late summer. Items with frequencies never exceeding 5% are not listed

Food Item	Species					
	Ord's kangaroo rat	Chisel-toothed kangaroo rat		Great Basin pocket mouse		
	Raft River Valley	Raft River Valley	Elmore Desert	Elmore Desert	Raft River Valley	Murphy Hot Springs
Seeds						
Halogeton....	27	3	0	0	0	0
Shadscale.....	0	5	0	0	0	0
Tansy mustard	11	14	0	0	0	0
Peppergrass..	15	3	0	0	8	0
Tickweed.....	15	4	29	30	23	1
Prickly pear..	8	11	0	0	8	0
Salt sage.....	4	7	0	0	0	0
Grass........	30	3	58	93	62	93
Winterfat....	0	0	46	2	0	0
Plantain......	0	0	0	0	0	23
Leaves						
Grass........	23	0	0	0	0	0
Shadscale.....	0	54	32	0	0	0
Halogeton....	13	18	0	0	0	0
Peppergrass..	11	3	0	0	8	0
Salt sage.....	0	7	0	0	16	0
Russian thistle	0	0	0	0	8	0
Miscellaneous						
Unidentified material......	4	3	0	16	16	16
Fungi........	0	0	0	9	0	0
Sample Size.....	71	76	28	43	13	91

The grass seeds in the cheek pouches of the rodents trapped in the Elmore Desert were almost entirely downy chess. The seeds of crested wheatgrass were the most common food item in the cheek pouches of Great Basin pocket mice trapped near Murphy Hot Springs.

The frequency of food items in the cheek pouches of the 2 kinds of kangaroo rats decreased progressively from early spring into summer. Of the Ord's kangaroo rats trapped in the Raft River Valley during April, June, and August, 59, 36, and 24% respectively carried food material in the cheek pouches. Of the chisel-toothed kangaroo rats trapped during these same months, 63, 42, and 26% respectively carried food material in their cheek pouches. Applying the difference in proportions test (Dixon and Massey 1951), the use of the cheek pouches by both species was significantly less ($P < .05$) in August than in April.

Discussion

Most species of rodents appeared to be opportunistic in their feeding, subsisting on a variety of foods and utilizing the different kinds as they became available. The phenology of several plants governed the availability of certain important food items. During April most of the rodents relied heavily on the seeds of halogeton for food. In June, with the flowering and fruiting of peppergrass and tansy mustard (*Descurainia pinnata*), the seeds of those plants became important constituents in the diet of several rodents. In August, prickly pear (*Opuntia*) seeds, available for the first time during the year, became an important food item, particularly for the least chipmunk and the deer mouse.

The availability of arthropods used as food is also influenced by changes in life histories. As an example, lepidopterous larvae are no longer available for use as food after metamorphosis.

One rodent, the chisel-toothed kangaroo rat, exhibited a preferential use of a single food item. This kangaroo rat subsisted almost exclusively on the leaves of shadscale during the early spring and into the summer. Eighty % of the animals which were examined had eaten shadscale leaves. In the Raft River Valley, chisel-toothed kangaroo rats were most frequently trapped in stands of shadscale. Depletion of shadscale areas through insect depredations and grazing has had a disastrous effect on the population density of this rodent. Again applying the difference in proportion test, the probability of trapping chisel-toothed kangaroo rats in the depleted stand of shadscale was significantly less ($P < .05$) than in a stand of shadscale in better condition.

Lepidopterous larvae were an important part of the diet of 3 insectivorous rodents, the deer mouse, the least chipmunk, and the western harvest mouse. These rodents may exert some control of a snout moth (*Eumysia* sp.) which has been reported by Tisdale and Zappetina (1953) to cause serious damage to shadscale.

The heavy use of the seeds and leaves of halogeton by rodents during the spring and early summer is of interest because of the known toxicity of that plant. Halogeton synthesizes oxalates and the salts of oxalic acid are the constituents responsible for its toxicity. Soluble oxalate concentrations have been reported to vary from 1.59 to 5.06% of the dry weight of the stems and from 19.53 to 32.81% of the dry weight of the seeds, sepals, and leaves (Dye 1956). The seeds and seed bracts are relatively lower in oxalates than the leaves (Cook and Gates 1960). Oxalate concentrations are highest in June and decrease progressively thereafter (Morton *et al.* 1959).

The factors that permit the use of halogeton seeds and seedlings as food by rodents during the spring and early summer were not determined. The ingestion of other foods along with the halogeton may have rendered it innocuous. Livestock can consume twice the lethal dose without injury if native forage is taken along with the halogeton (Stoddart *et al.* 1951). Leaching of the soluble oxalates from the seeds during the winter months may have reduced their toxicity to safe levels. Simulated leaching in the laboratory significantly reduced the oxalate content of halogeton (Cook and Gates 1960). Finally, rodents may show a greater tolerance to oxalates than do livestock.

SUMMARY

A study was conducted during April, June, and August, 1957, in the Raft River Valley, Cassia County, Idaho, to gain information on the seasonal diets of rodents and their effect on forage palatable to livestock. Secondary studies were conducted at 3 other localities in southern Idaho.

Stomach contents were examined microscopically and the contents of cheek pouches were saved and identified.

Deer mice, western harvest mice, and least chipmunks were found to rely heavily on arthropods for food. Ord's kangaroo rats ate a variety of leaves and seeds. Chisel-toothed kangaroo rats fed almost exclusively on the leaves of shadscale. The foods used by 6 other infrequently trapped species are also reported.

Probably as a result of availability, the frequency of grass and grass seeds in the stomachs of deer mice trapped outside a livestock exclosure was much reduced from the frequency of use of these items within the exclosure.

The food material carried in the cheek pouches of kangaroo rats was much the same as that found in the stomachs at the time of trapping. There was a progressive decrease in the use of cheek pouches to carry food material by 2 kinds of kangaroo rats from early spring into the summer.

Most of the rodents inhabiting shadscale and sagebrush associations subsist on diverse kinds of food. Availability appears to govern the use of most foods. The chisel-toothed kangaroo rat, however, was found to be closely associated with shadscale stands both in distribution and in diet. The population density of this rodent is significantly reduced by depletion of areas supporting shadscale.

Certain rodents may be important in controlling an insect pest of shadscale.

Halogeton seeds and seedlings constituted a large part of the food eaten by most rodents during the spring and early summer. The supplemental use of other foods, the leaching of the toxic constiuents during the winter months, or a tolerance of rodents to oxalates may be the factors responsible for nullifying the toxic effects of halogeton. Further study is necessary to determine how halogeton is rendered safe for use as food by rodents.

REFERENCES

Baumgartner, L. L. and A. C. Martin. 1939. Plant histology as an aid in squirrel food-habits studies. Jour. Wildl. Mgt. **3**: 266-268.

Cook, C. W. and D. H. Gates. 1960. Effects of site and season on oxalate content of halogeton. Jour. Range Mgt. **13**: 97-101.

Dixon, W. J. and F. J. Massey, Jr. 1951. Introduction to statistical analysis. McGraw-Hill Book Co., Inc., New York. 370.

Dusi, J. L. 1949. Methods for the determination of food habits by plant microtechniques and histology and their application to cottontail rabbit food habits. Jour. Wildl. Mgt. **13**: 295-298.

Dye, W. B. 1956. Chemical studies on *Halogeton glomeratus.* Weeds **4**: 55-60.

Fautin, R. W. 1946. Biotic communities of the Northern Desert Shrub Biome in western Utah. Ecol. Mono. **16**: 251-310.

Morton, H. L., R. H. Haas, and L. C. Erickson. 1959. Oxalate and mineral contents of *Halogeton glomeratus.* Weeds **7**: 255-264.

Piemeisel, R. L. 1945. Natural replacement of weed hosts of the beet leafhopper as affected by rodents. USDA Circ. No. 739.

Stoddart, L. A., H. Clegg, B. S. Markham, and G. Stewart. 1951. The halogeton problem on Utah's ranges. Jour. Range Mgt. **4**: 223-227.

Tisdale, E. W. and G. Zappetini. 1953. Halogeton studies on Idaho ranges. Jour. Range Mgt. **6**: 225-236.

COMPARISON OF TEMPERATURES INSIDE AND OUTSIDE TWO TREE DENS USED BY RACOONS

HOWARD J. STAINS
Department of Zoology, Southern Illinois University, Carbondale

The environment of an animal's den is important to the occupant as it spends a large percentage of its time there. Despite this importance, the microclimates of the ground dens of larger mammals and of tree dens have been neglected.

The variation in temperature in the den can be determined by installing the bulb of a recording thermometer. By use of this technique, the activity of a mammal occupying the den also can be studied. However, before an animal's activity can be properly interpreted, the investigator must understand the relationship between inside and outside temperatures so that changes caused by the animal entering and leaving the den can be recognized. The objective of the present study was to determine the thermal characteristics of a tree den.

Recordings were made at 2 raccoon dens in trees, each den being studied in different years. Den number 1 was a tree-den from which a litter of 4 raccoons had been removed the previous year. It was in a large red maple (*Acer rubrum*) located in a wooded area on Little Galum Creek, Perry County, Illinois. The tree was approximately 60 ft high, 4 ft in diameter, and 150 ft from the creek proper which was wooded on both sides in a strip approximately 700 ft wide. Three dens were in this tree. The lower den, some 15 ft above the ground, was studied. The entrance was 5.5 inches high, 4.5 inches wide and faced to the north. This entrance opened vertically into a cavity 29 inches in diameter, 14.5 inches from the entrance to the bottom, and 5 ft from the entrance to the roof. A 3-inch wall of living wood insulated the cavity on all sides.

Den number 2 was in a large river birch (*Betula nigra*) which later became occupied by a female raccoon who remained to have a litter. This den-tree was located in a mature woods some 200 ft from Little Crab Orchard Creek, Jackson County, Illinois. The den, approximately 20 ft above ground, had 2 openings at the top, a 13-inch entrance to the west and an 11-inch entrance to the northeast. The cavity was 22 inches in diameter and 4 ft deep. A 3-inch wall of living wood insulated the den. However, this 2nd den did not have the insulating properties of that of the first den largely because of the large entrances located at the top.

METHOD

Temperatures were taken by a 7-day recording thermometer, Bristol series 500, having 2 high-sensitivity thermometer bulbs, two 5-foot extension cables, and 2 recording pens. This instrument was housed in a plywood box attached to the south side of each tree level with the bed of each den. The thermometer bulb for recording outside temperatures was attached between the box and the tree, and the 2nd bulb was placed on the bed of the den. This was done by drilling a ¾-inch hole through the tree and inserting the element through the hole.

RESULTS

Temperatures inside and outside both dens follow quite similar patterns, being highest in summer and lowest in winter. The major difference between den temperatures and outside temperatures was that the den temperature was less variable (Tables I and II). This would be expected owing to the insulating properties of the tree. Usually the fluctuation of den temperature remained within the extremes of the outside temperature unless the latter changed drastically over a short period of time. The average hourly temperature in the den remained approximately the same as the average hourly temperature outside showing that the actual difference between these 2 environments was in the greater uniformity of the inside temperature. The magnitude of temperature change outside the den during a day was, on the average, 5.4°F for each degree change inside the den throughout the year at den number 1 (Table I) and 4.5°F at den number 2 (Table II). The data from den 2 do not include April and parts of March and May as the den was occupied by a raccoon and her litter during this period. The more uniform temperature of den 1 is an indication of its being better insulated.

TABLE I. Average hourly temperatures of each month out side and inside tree den number 1, 1958-59

Month	OUTDOOR				IN DEN				Av. Change Outdoor/1° in Den
	Max.	Hr. Av.	Min.	Range	Max.	Hr. Av.	Min.	Range	
June	76.8	68.6	59.4	17.4	71.6	69.9	68.0	3.6	4.9
July	79.0	73.2	67.4	11.6	75.2	74.2	73.1	2.1	5.6
August	80.9	73.7	66.3	14.6	75.7	74.6	73.3	2.4	6.0
September	75.9	67.3	59.4	16.5	70.1	68.5	67.0	3.1	4.9
October	70.3	57.9	47.9	22.4	60.2	56.3	55.7	4.5	4.7
November	57.5	46.2	35.9	21.6	50.3	47.2	45.5	4.8	4.5
December	37.9	29.8	21.3	16.6	28.7	28.3	28.0	0.7	22.8
January	34.1	27.1	17.5	16.6	28.0	27.4	26.2	1.8	9.4
February	45.3	35.9	26.2	19.1	32.1	30.7	29.5	2.6	7.5
March	56.3	45.3	33.7	22.6	45.4	41.9	39.5	5.9	3.8
April	67.9	56.8	44.5	23.4	58.7	55.6	52.9	5.8	4.0
May	76.7	67.8	60.3	16.4	69.2	68.0	66.5	2.7	6.0
YEARLY	62.7	53.7	44.3	18.4	54.6	53.0	51.2	3.4	5.4

TABLE II. Average hourly temperatures each month outside and inside tree den number 2, 1959-60

Month	OUTDOOR				IN DEN				Av. Change Outdoor/1° in Den
	Max.	Hr. Av.	Min.	Range	Max.	Hr. Av.	Min.	Range	
August	84.0	75.2	69.4	14.6	76.1	74.5	72.9	3.2	4.6
September	76.6	66.3	57.6	19.0	69.4	67.2	64.9	4.5	4.2
October	67.1	57.0	47.4	19.7	56.6	54.3	52.5	4.1	4.8
November	49.7	39.1	28.8	20.9	39.6	37.4	35.1	4.5	4.6
December	43.5	39.1	31.3	12.2	34.4	32.6	30.4	4.0	3.1
January	42.2	35.9	30.4	11.8	32.4	30.9	29.8	2.6	4.5
February	40.0	32.9	26.4	13.6	29.7	28.3	27.4	2.3	5.9
March	44.0	36.2	26.7	17.3	35.8	32.4	29.9	5.9*	2.9
April	71.9	57.9	48.8	23.1	66.2	58.7	53.1	13.1*	1.8
May	72.4	62.5	52.7	19.7	78.1	66.9	58.2	19.9*	.9
June	81.9	71.8	61.3	20.6	67.8	65.1	61.8	6.0	3.4
Yearly including occupancy:	60.9	48.5	43.5	17.4	53.2	49.7	46.8	6.4	2.7
Yearly less time of occupancy:	58.5	51.3	42.2	16.3	48.8	46.9	45.2	3.6	4.5

* Raccoon entered den on March 24, had a litter, and remained until the evening of May 23, 1960.

The greatest deviation between inside and outside temperature was in December, 1958 when the temperature outside changed 22.8 degrees for each degree change recorded inside (Figure 1). This small variation in den temperature resulted from the formation of ice in the damp litter at the bottom of the den thus creating a constant temperature near the location of the recording element. Average hourly temperatures for the period December through much of February in den 1 and late February and early March at den 2, showed these effects of freezing weather on temperature change within the den. Temperatures never remained high enough to melt all the ice and thus den temperatures tended to remain below the freezing point. Variations of temperature inside and outside the den in the other months followed similar patterns. In March there was a 3.8 degree change outside to each degree change in den 1 and in April a 4.0 degree change outside for each degree change inside. Den 2, being poorly insulated, showed this type of curve most of the year. This close correlation at den number 1 may be the result of the absence of leaves allowing the wind to influence the den temperature more readily. The presence of the litter of young raccoons at den number 2 during these months made interpretations of the above nature impossible in 1960.

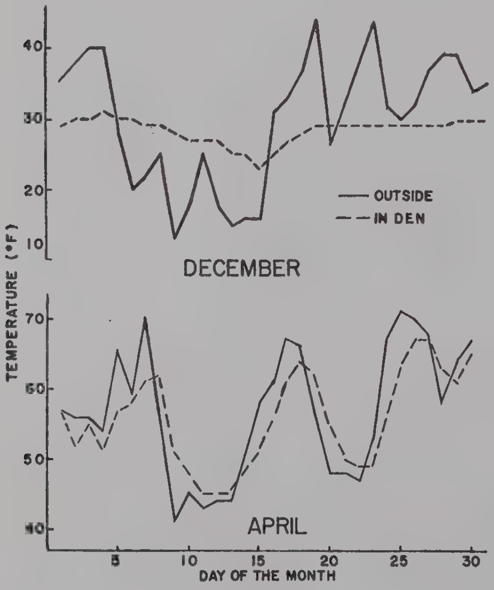

FIG. 1. Typical relationships of outside temperatures and den temperatures in winter (December) and at other times of the year (April). Recordings made at den number 1.

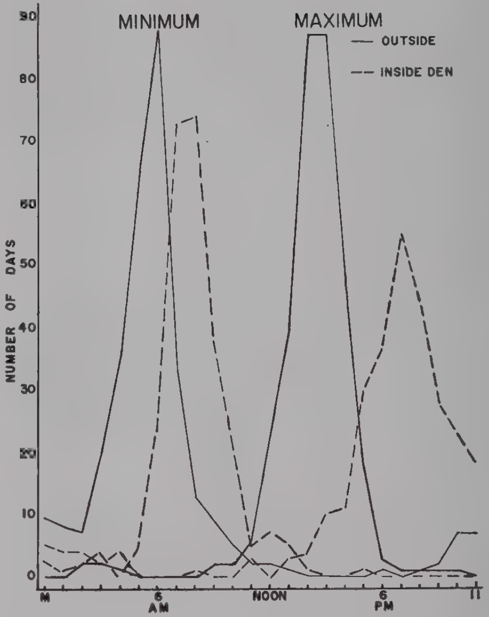

FIG. 2. The time of day that outside and in-den maximum and minimum temperatures were recorded at den number 1.

TABLE III. Time lag between temperature peaks outside and in the dens

Month	Hours Between Peaks			
	Rising Temp.		Falling Temp.	
	Den 1	Den 2	Den 1	Den 2
June	5.6	1.9	1.9	.3
July	4.7	—	3.6	—
August	5.7	3.3	2.4	0.8
September	6.4	2.7	2.8	1.2
October	5.4	2.8	2.3	1.5
November	5.5	3.5	2.9	3.3
December	3.9	3.3	3.2	0
January	5.4	5.7	4.3	4.0
February	3.3	5.1	3.0	4.3
March	5.2	2.6	3.6	2.0
April	5.2	*	2.6	*
May	4.6	*	3.6	*
YEAR	5.2	3.2	3.0	1.6

* Omitted because of litter in den.

The response of den temperature to changes in outside temperature was slow, the maximum and minimum den temperatures being reached later than outside temperatures (Figure 2). This time lag was greater when outside temperatures were rising than when they were falling (Fig. 2 and Table III). The monthly average hourly time lag on rising temperatures at den 1 ranged from 3.3 to 6.4 (average 5.2) hours, and on falling temperatures from 1.9 to 4.3 (average 3.0) hours. At den 2, as a result of its being poorly insulated, the time lag on rising ranged from 1.9 to 5.7 (average 3.2) hours, and on falling temperatures from 0 to 4.3 (average 1.6) hours. These figures indicate that warming of a den proceeds more slowly than does cooling, taking approximately twice as long between inside and outside peaks on rising as opposed to falling temperatures.

There was no shift in the time of day of maximum and minimum temperatures outside and inside the den from month to month. The minimum outside temperature usually occurred between 5 and 6 AM; the maximum between 2 and 3 PM in both years (Fig. 2). The minimum den temperature usually occurred between 7 and 8 AM; the maximum between 6 and 8 PM at den number 1 (Fig. 2), and between 6:30 and 8 AM and 4 and 6 PM at den number 2. Den and outside temperatures usually were identical sometime between 7 and 9:30 AM on rising temperatures and between 5:30 and 8 PM on falling temperatures.

The highest temperature recorded outside den 1 was 89°F on June 8, 1958 (the den temperature was 75°F on this date) and at den 2, 90°F on June 4, 1960 (the den temperature was 72°F on this date. The highest inside den 1 was 79.5°F on August 15, 1958 (the outside temperature was 83.5° on this date); the highest inside den number 2 was 79°F (discounting the time the litter was inside when temperatures went as high as 91°F) on August 5, 23, 24, 25, and 29, 1959 (the outside temperatures were 85, 88, 88, 87, and 88°F on these dates). The fastest rise in outside temperature occurred on November 20 and December 7, 1958, when the temperature rose 11.5° in one hour. The record rise of 1958 was surpassed 3 times in 1959-60; a 17° rise in one hour on September 13, a 14° rise on April 19, and a 15° rise on April 22. The fastest rise in the den was never more than one degree in one hour at den number 1; any faster rise indicated the presence of some animal. The same was true of den number 2 with 9 exceptions when a rise of 1½° (5 times), 2° (3 times) and 3° (once) occurred within one hour. Response of the element on entrance of an animal produced an almost vertical rise which never occurred in the changes of over 1 to 3° mentioned above. This rise could be as great as 25° in one hour depending on the closeness of the animal to the element and the size of the animal. In addition, numerous peaks were apparent as the animal moved about the recording element.

The lowest temperatures recorded outside were —4°F on January 4 and 5, 1959, and —6°F on March 4, 1960; the lowest inside den number 1 was 21°F on January 5, 1959, and in den number 2 it was 20°F on March 5, 1960. The fastest drop in outside temperature was on November 17, 1958, and November 13, 1960, when the temperature fell 23° in one hour. The fastest fall in den number 1 was 2° in one hour on November 25, 1958, and April 8, 1959, and at den number 2 a fall of 2° in one hour was recorded 13 times and 3° in one hour on August 16, 1960. Exit of an animal also was accompanied by a rapid fall but more characteristic was the absence of numerous peaks always present when an animal was in the den.

The greatest continuous change in outside temperature occurred on February 10 and 11, 1959, when the temperature fell 46° in 24.5 hours (the temperature at den number 1 fell 10° at this time), and 43° in 21.5 hours on November 14-15, 1959 (the temperature at den number 2 fell 14° at this time). The greatest continuous change in temperature in den number 1 was from November 17 to 19 when the temperature fell 20° in 37 hours (the outside temperature fell 44° at this time), and in den number 2 from November 5 to 7 when the temperature fell 30° in 52.5 hours (the outside temperature fell 51° at this time). The time between in-den peaks and lows was prolonged more than 24 hours on 37 occasions in 1958-59 and on 53 occasions in 1959-60 even though fluctuations occurred outside. These occasions were during periods of prolonged trends of rising or falling outside temperatures. The minimum lows and maximum peaks in the den ranged from 31 to 276 hours apart in 1958-59 and from 27 to 150.5 hours apart in 1959-60. Twenty-three of these occurred during rising temperatures in 1958-59 and 28 in 1959-60; and 14 during falling temperatures in 1958-59 and 25 in 1959-60 with most of them being found in December (456 hours of no peaks in 1958 and 539 hours in 1959), January (547.5 hours in 1959 and 557 in 1960), and February (339.5 hours in 1959 and 619 in 1960). These also were the months of the greatest differences in range of temperature in the den and outside, or the months of the smallest change of in-den temperatures because of freezing conditions affecting the sensitivity of the element.

SUMMARY

Simultaneous records of temperature were obtained inside and outside 2 tree dens. One den was poorly insulated, the other well insulated. Both dens were at one time utilized by raccoons to raise litters. Inside and outside den temperatures followed similar patterns and were approximately the same in average hourly temperatures, but inside temperatures varied less than outside temperatures. A yearly average change of 5.4°F outside caused an average change of 1.0° in den 1 (well insulated) and a change of 4.5°F outside caused a 1° change in den 2 (poorly insulated).

There was a temperature lag between den and outside temperatures. This lag was greater during rising temperatures than falling temperatures. The minimum outside temperature usually occurred approximately 2 hours before the minimum temperature was reached in both dens, the maximum approximately 5 hours before the maximum at den number 1 and 2.5 hours before that at den number 2.

During periods of continuous trends, up or down, of temperatures outside the den, the den temperature often continued to a uniform prolonged peak or trough for as long as 276 hours. The fastest rise in the den was never more than one degree per hour in den number 1. In general, the same was true of den number 2. The fastest fall usually was no more than 2° per hour. Outside the fastest rise was 11.5° in one hour in 1958 and 17° in 1959, the fastest fall, 23° in one hour, occurred once in 1958 and 1960. Entrance to the den by a mammal caused an immediate rise followed by oscillating temperatures caused by the nearness of the animal to the element.

LUNAR PERIODICITY IN SPAWNING AND LUMINESCENCE IN *ODONTOSYLLIS ENOPLA*

Robert E. Markert, Betsy J. Markert, and Nancy J. Vertrees
Bermuda Biological Station, Bermuda[1]

The relationship between the moon and periodicity in the breeding of marine animals is beautifully illustrated by the luminescent Bermuda annelid, *Odontosyllis enopla.* The monthly swarming of this worm has attracted the attention of several investigators (Galloway and Welch 1911, Huntsman 1948) who have noted that the appearance of the worms may be predicted with extraordinary accuracy. The swarming of Odontosyllis has been reported during most months of the year although they appear in greater numbers during the summer months. Beginning a day or two after the full moon they spawn on several successive nights during an interval of about 20 minutes. Females appear first, swimming in narrow circles at the surface and emitting a bright greenish light. The emitted light apparently attracts the males which, while they are swimming toward the females, give off short flashes of light.

Commonly several males will be attracted to a single female and all the worms will then rotate in a tight circle while discharging their gametes into the water. Luminescence continues during the release of the gametes and in fact the eggs, at least, are accompanied by a secretion that produces a luminous cloud in the wake of the female.

The worms pose the problem of periodic behavior in a striking manner. Since they are active throughout the year their behavior is not conspicuously seasonal but is rather tied to a lunar periodicity. The triggering mechanism by which spawning and light emission are stimulated has not been experimentally investigated but the reported precision in the time of appearance of the worms after sunset suggests that a fixed (and relatively short) period of darkness may initiate spawning behavior. Any interpretation must depend upon accurate data. Since no precise data have been published on spawning behavior in *Odontosyllis enopla* the present investigation was undertaken to gather such data.

Materials and Methods

In June 1959 at the monthly period of spawning a survey was made of several promising areas around the shores of Bermuda. Considerable variation in the abundance of luminescent worms was noted along the coasts. In some areas virtually no worms appeared and in other areas they were exceedingly numerous. Favored areas were in shallow water 10-20 ft deep covering a rocky bottom. A cove on the north side of St. George's Island opposite Mullet Bay was selected as fairly representative of those areas in which worms appeared. The area selected for observation was naturally marked off by rocks jutting from the water and lay at the foot of steep cliffs. From the vantage of these heights an area of 2600 sq ft could be kept under close surveillance by one observer while others recorded his observations. The area was shallow, up to 10 ft deep, and had an irregular rocky bottom. The water was very clear and on calm days the bottom throughout the area could be seen in sharp detail from the cliffs above. The number of luminescent female worms appearing each minute was recorded for every night during July 1959. Typically a female worm appears at the surface giving off a greenish light for several seconds while swimming rapidly in narrow circles. Usually males soon appear and encircle the female while giving off short intermittent flashes of light. Gametes are discharged into the water where fertilization occurs. The eggs are enshrouded in a luminescent cloud. The luminescence of the female is much greater than that of the male and is easily distinguished from that of the male. A female may luminesce more than once particularly if no males appear. Such females, if they remained in the area, would be counted at each luminescence as an additional worm. This error seems unavoidable but in any event should apply equally to each night's observations and thus would not seriously impair the data on periodicity.

Results

The results of these observations in the selected area are presented in Figures 1-3. No worms appeared between the new moon and the full moon—a period of about two weeks. Worms made their initial appearance on the first night after the full moon and on the 3rd night reached a peak of abundance. On succeeding nights the number declined steadily until only one worm was seen on the 12th night after the full moon and none on the following nights.

The data obtained on July 22, the night on which the worms were most abundant, are presented in Fig. 1. It is evident that the rate of appearance of the worms during the night shows a symmetrical distribution with a peak rate of appearance at 56 minutes after sunset. The entire display, save for one laggard, was finished in 15 minutes. It is this precision that led to the suggestion that one could set his watch by the worms, and well he might, with remarkably small error.

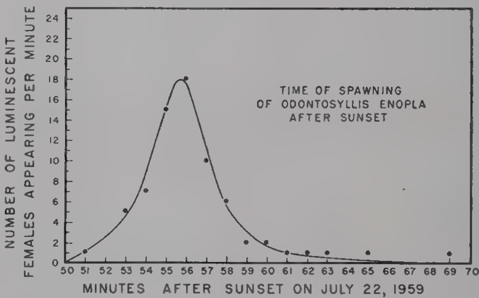

Fig. 1. The number of females observed to begin luminescing and spawning during each minute after sunset plotted against the time of appearance. The greatest number of worms appeared between 55 and 56 minutes after sunset.

A different plot of the data to compare the behavior of the worms on the four nights during which they appeared most abundantly is shown in Fig. 2. Although there is some variation in the length of the dark period after sunset that is required to induce spawning, the occurrence of spawning females on any one night follows the same distribution as was evident on the most prolific night plotted in Fig. 1.

---

[1] Contribution No. 283 from Bermuda Biological Station.

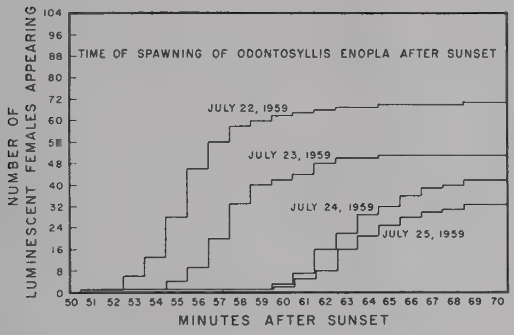

FIG. 2. A cumulative plot of the number of luminescing female worms that appeared on each of the 4 most prolific nights in July. The curves are similar although the provoking period of darkness following sunset increases slightly on successive nights.

Figure 3 relates the spawning of Odontosyllis to phases of the moon. It is obvious that the 3rd night after the full moon is the preferred night for spawning. However at least a few worms can be observed luminescing on about half the nights each month. The favored nights have in common a period of about one hour of darkness following sunset during which no moon is visible. This dark period may be the triggering stimulus for the nuptial swim.

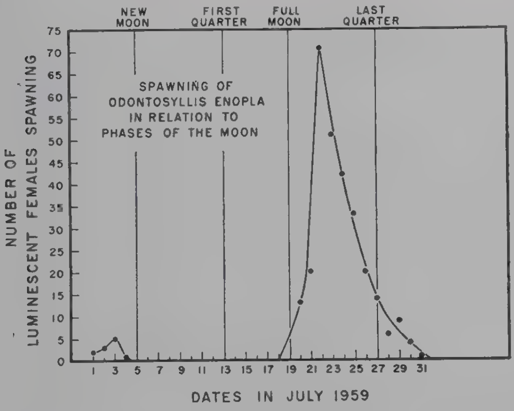

FIG. 3. The number of female worms appearing during each night of July is shown in reference to the phases of the moon. The nights during which worms appeared have in common at least one hour of moonless darkness following sunset.

During spawning several males usually rotate rapidly around a single female. This fact casts doubt on a one to one sex ratio. Moreover when several thousand worms were collected in nets with the aid of light shone on the water only a very few of these proved to be females. Although males rather than females would be expected to respond to light, the area from which the worms was collected never gave any evidence of containing as many females.

DISCUSSION

Although popular accounts may exaggerate the precise predictability of Odontosyllis behavior it is nevertheless impressive. The provoking stimulus is probably a period of darkness following sunset (about 56 minutes). The tides are so small at Bermuda that they are not likely to be involved particularly since the worms can appear at any stage of the tide, that is, at whatever stage of the tide happens to occur at 56 minutes after sunset on the fertile days of the lunar cycle.

Several previous investigators have made general observations on the behavior of Odontosyllis but have not collected precise data. However, Huntsman (1948) clearly postulated an hour of moonless night following sunset as the stimulus to spawning. The present data support his suggestion. Both males and females respond to the environmental stimulus, whatever it may be, independently of one another. However, the males exhibit an additional positive response to light. They are attracted by the light emitted by the females but are equally stimulated by the beam from a flashlight. No evidence for a positive response to light by the females was obtained although they are stimulated by the presence of the males to release their eggs. An examination of the anatomy of males and females provides few clues to their behavior. Males are much smaller, but have larger eyes, in keeping with their sensitivity to the light given off by females. A detailed discussion of Odontosyllis anatomy may be found in Galloway and Welch (1911). The cellular and physiological basis for the luminescence has not been demonstrated but preliminary studies on the nature of the luminescent system have been reported by Harvey (1952, pp. 218-223). All segments of the female become luminous when she is agitated, and the release of the eggs is accompanied with a luminous secretion in which light emission continues for several seconds. Odontosyllis may easily be maintained in the laboratory and thus should provide good material for an experimental analysis of spawning and luminescent behavior in relation to external stimuli.

ACKNOWLEDGMENTS

Work performed under contract No. AT (30-1)—2157 with the U. S. Atomic Energy Commission. We wish to acknowledge the interest and guidance of Dr. C. L. Markert during the course of this investigation.

REFERENCES

Galloway, T. W. and P. S. Welch. 1911. Studies on a phosphorescent Bermudan annelid, *Odontosyllis enopla* Verill. Trans. Amer. Microscopical Society **30**: 13-39.

Harvey, E. Newton. 1952. *Bioluminescence.* New York, Academic Press.

Huntsman, A. G. 1948. Odontosyllis at Bermuda and lunar periodicity. Jour. Fisheries Res. Board Canada **7**: 363-369.

ECOLOGICAL CHANGES IN THE PONDEROSA PINE FOREST OF CEDAR VALLEY IN SOUTHERN WASHINGTON[1]

Harold Weaver

The *Pinus ponderosa* forest of Cedar Valley on the Yakima Indian Reservation east of the Cascade Range in southern Washington has experienced profound ecological changes over the past century. It was originally a magnificent, park-like forest with a clean, grassy forest floor (Fig. 1). Now there remain but scattered, patchy remnants of this original forest.

An almost universal understory of young trees now characterizes the valley. Extensive large-pole size groups of pine 6-10 in. dbh have thus far grown well. Equally extensive younger age classes, however, are now so dense that they are growing poorly. These stands are adversely affecting the growth rate and vigor of the remaining mature trees through competition for soil moisture. Fir (*Abies amabilis* & *A. grandis*) reproduction is predominant at higher elevations. Fire hazard has increased tremendously.

These changes are typical of those that are occurring over more extensive portions of the Ponderosa Pine Region. Fire was an important ecological factor in the primeval ponderosa pine forest and changes have resulted largely from early day over-grazing by domestic stock and from attempts at total fire exclusion (Weaver 1943, 1951, 1955, 1958; Cooper 1960). In Cedar Valley there has been extensive killing of the mature overstory by epidemics of the defoliating pine butterfly (*Neophasia menapia*) and the western pine beetle (*Dendroctonus brevicomis*).

Cedar Valley and surrounding areas provide an exceptional opportunity to study effects of great insect epidemics and the ecological changes caused by the white man. These changes can be correlated with the historical record. My purpose, therefore, is to present a more detailed account of the changes.

Description of Area

Cedar Valley includes approximately six townships in the southwestern portion of the Yakima Indian Reservation. Three principal streams, Trout Creek, White Creek and Summit Creek, drain southwestward into the Klickitat River, a short distance beyond the reservation boundary. In their lower extremities these streams have incised deep, sharp canyons. General elevation varies from approximately 2000 ft above sea level, in the southern portion, to 3500 ft in the north.

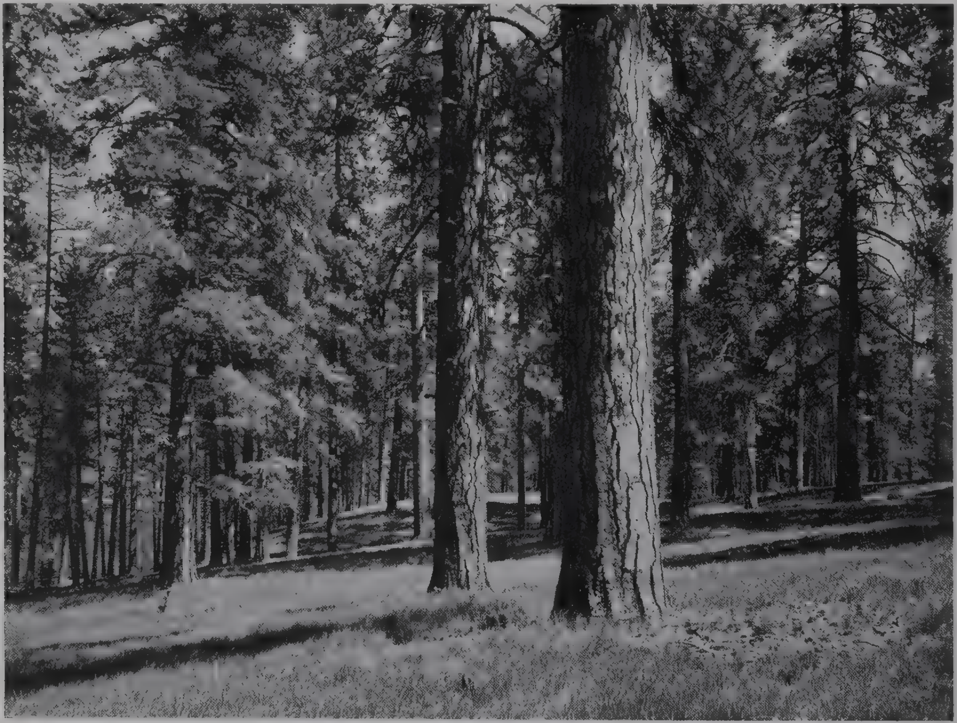

Fig. 1. The open parklike appearance still prevails on limited portions of the ponderosa pine forest in the upper Klickitat drainage. Ground cover consists principally of pinegrass. Almost all of Cedar Valley once looked like this.

---

[1] This article represents the author's views and is not to be regarded as an official expression of the attitude of the Bureau of Indian Affairs on the subject discussed.

A number of isolated volcanic buttes and cinder cones are scattered throughout the valley. Cinder cones also occur in the Simcoe Mountains to the east and northeast. A spur of these mountains bounds the valley to the southeast. Through a pass in this ridge early settlers gained access to the valley, but until advent of the bulldozer the Klickitat and its side canyons remained an impassable barrier to wheeled traffic.

Another mountain ridge to the west and northwest separates the valley from other portions of the Klickitat drainage. Approximately 15 miles beyond this ridge, across the Klickitat River canyon, is Mt. Adams.

Soil is coarse loess, deposited over basalt rock, and generally is deep and well drained. Basalt outcrops occur along canyon rims.

Douglas fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*) and firs are associated with ponderosa pine at higher elevations, on north slopes and near stream courses. Limited stands of lodgepole pine (*Pinus contorta*) occur on poorly drained areas and high in the Simcoe Mountains. Black cottonwood (*Populus trichocarpa*) and western red cedar (*Thuja plicata*) occur occasionally along stream courses. It is estimated that original merchantable volume averaged in excess of 15,000 bd ft per acre. Ground cover, under the pines, was dominated by a luxuriant stand of pinegrass (*Calamagrostis rubescens*).

EARLY CONDITIONS

Stand structure and composition of the primeval ponderosa pine forest reflect the important role played by frequent, periodic fires. Without disturbance of the pinegrass ground cover, tree seedlings were most apt to die from competition or from the next creeping fire. Fire was important by providing disturbance by burning trees killed by insects, lightning, or windthrow. The recurrent fires that reduced this material to ashes cleared the grass cover and exposed the mineral soil, a suitable bed for germination of seedlings. With occasional good seed crops and favorable moisture the tree seedlings grew and by the time the ground cover reestablished itself, some were large enough to survive the fires. Ponderosa pine, being relatively more fire resistant, had a considerable advantage over associated tree species in surviving these fires. Thus openings in the overstory were restocked with young pines at all elevations. This explains the characteristic even-aged grouping of ponderosa pines by various age classes (Weaver 1943, 1951, 1955; Cooper 1960).

I surmise that some extensive even-aged stands of pine resulted from devastating insect attacks, followed by fires (Weaver 1943). Changes following the butterfly and pine beetle attacks in Cedar Valley illustrate how even-aged stands started in earlier days. Even before the butterfly attacks there is evidence that the mature Cedar Valley forest was predominantly even-aged.

Scars, or "cat faces," on many older trees indicate that fires occurred frequently until the early 1900's. The fire scarred section in Figure 2 is typical of many thousands throughout Cedar Valley and adjacent areas. This section was cut from the butt of a pine of intermediate crown class and of 16 inches dbh, harvested near Trout Creek in November, 1959. It indicates that 13 different fires attacked this particular tree from 1807 through 1935.

Some fires probably started from dry lightning storms that are frequent during the summers and doubtless many were started by Indians. Fires occurred as frequently as

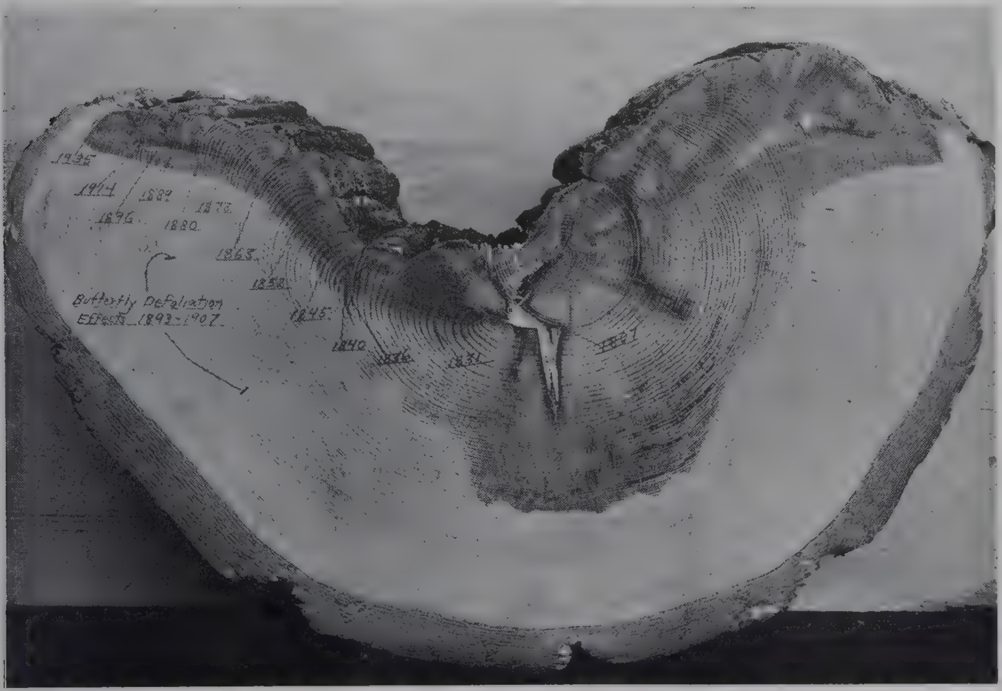

FIG. 2. Fire-scarred section cut from butt of pine harvested in November, 1959. Scars indicate that at least 13 different fires burned during the period 1807-1935 inclusive. Band of very narrow rings, from 1893-1907 inclusive, apparently resulted from severe defoliation by white pine butterflies.

weather and fuel conditions were favorable and whenever lightning or humans ignited them.

Early Activities of White Men

White men entered the reservation area before 1855 (Relander *et al.* 1955). It is probable that grazing pressure by domestic stock developed on the mountain ranges at a somewhat later date than it did on the lower bunch grass ranges. Saxton (1914) reported that sheep grazing in Cedar Valley had started about 1880. The first settlers were from the Missouri River Valley. Crops planted on clearings frequently failed. Frost sometimes occurs during every month of the year. For a time sawmills proved more profitable than agriculture. Several waterpower and steam sawmills were constructed (Clark 1954). Homesteaders eventually patented 27,000 acres (Neibel 1953).

Conditions in the valley at about this time were described in a letter by Agent Jay Lynch to the Commissioner of September 1, 1900. He reported that "From my knowledge . . . it contains the best pine timber in the state. . . . It is practically free from undergrowth (Fig. 1) and when not over-run with sheep is excellent summer pasture. It is well watered, with hundreds of springs and many small creeks . . . . There are about 25 settlers on this land who claim they have patents from the government. There are two sawmills . . . and thousands of sheep. Sheep camps are found on every creek and the whole tract is being used as a pasture by white people" (Neibel 1953).

Frosts and long winters eventually drove out the settlers. Between 1910 and 1926 all but two or three left the valley (Neibel 1953). The last settler left about 1933 and most of the patented lands have been purchased by a lumber company. Loggers have burned most of the settlers' buildings to prevent occupancy by unwanted transients.

The Butterfly Epidemic and Subsequent Changes

The epidemic of defoliating pine butterflies started in 1893. These insects were so numerous that they made the pines appear white. Streams were choked by the dead butterflies and travelers reported that horses and men were covered from head to foot with webs of the larvae. Defoliation continued through 1895, when the epidemic ended, probably due to wasp-like parasite (*Theronia fulvescens*) (Keen 1952, Meyer 1959).

The section in Figure 2 records effects of the infestation in the narrow growth rings beginning in 1893. They continue, however, until 1907. It may be that it took many years for the tree to recover from severe defoliation. Also it apparently was intermediate in crown position and was dominated by more vigorous neighbors, even after the epidemic. It may be also, that the epidemic lasted longer than 1895, as reported (Clark 1954).

Tree mortality was spotted and varied considerably. From 20-90% of the stand was killed and total loss amounted to nearly one billion board feet. The valley was visited in 1912 by an entomologist named Harvey, who found that in addition to extensive defoliation by the butterfly there was a severe epidemic of the western pine beetle. He attributed death of most of the trees to this insect (Keen 1952, Meyer 1959).

Seed from dying pines germinated on a mineral soil seed bed on the severely trampled forest floor and millions of little pines became established about 1900. These trees have since developed into the present extensive, even-aged large pole stands that cover a substantial portion of the valley (Fig. 3). They are characterized by a complete absence of larger, mature pines, or by a light overstory of these trees. Most of the original stand died during the butterfly epidemic and some of the survivors have been harvested during recent logging operations.

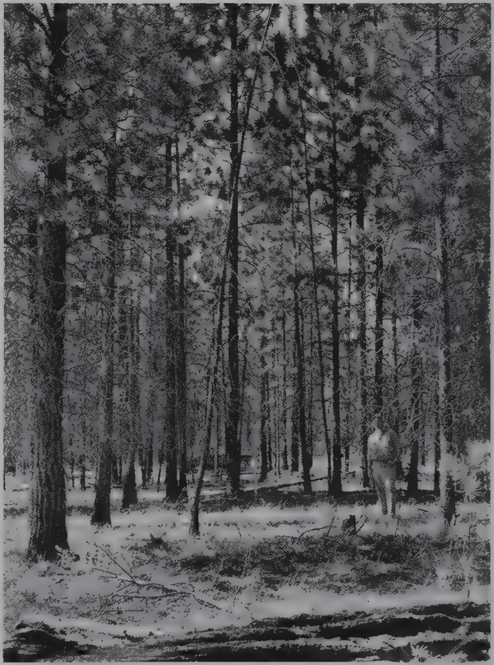

Fig. 3. Typical appearance of pine butterfly infestation area in 1958. Poles originated as seedlings about 1900. Stand was thinned by wild fire in 1913 and by a controlled burn in 1952, during slash disposal. Man stands in small, circular opening caused by burning pitch stump or log in 1913. Note fire scar facing opening on small crooked tree at left. Ground cover consists principally of pinegrass (*Calamagrostis rubescens*) and elk sedge (*Carex geyeri*).

The most significant characteristic of this even-aged pole stand is that almost everywhere over the valley it has been thinned by fires that burned in the early 1900's (Fig. 3). I have traveled extensively over Cedar Valley and all areas of this age class show evidence of fires that burned after establishment of the stand. There are small clearings and cleared lanes where logs and pitchy roots burned. The charred, largely fire-consumed remains of the original butterfly and beetle killed stand are everywhere. Fire scars on adjacent poles are still in evidence. Others are completely grown over and are revealed only by chopping or from increment cores which show that many of the surviving trees were less than one inch dbh when burned. The ground under these stands is still grassy and largely free of debris (Fig. 3).

There was abundant opportunity for these low intensity fires to start in the early 1900's. Stockmen and settlers were opposed to "brush" and to windfalls that impeded travel and impaired observation. Fire provided the most feasible means of removing these impediments. Besides it was considered that fire benefited the grass.

Saxton (1914) reported on fires in Cedar Valley that "Very seldom is reproduction entirely killed on extensive areas. Usually it is a process of thinning out the weaker and smaller specimens with more or less scorching of the older ones. . . . This is especially true in yellow pine." He reported that 16,000 acres burned in 1913 and 13,500 acres in 1914. Most fires burned in the butterfly killed area. He attributed these to white and Indian campers and reported that a sheep driveway was one of the greatest aids in preventing fires coming onto the reservation from the south. It checked 7 miles of fire front.

With advent of more effective fire control, there developed younger, exceedingly dense age classes of reproduction that in great part have not been thinned by fire. They occur in openings caused by pine beetle and butterfly epidemics. Pine beetles were severely epidemic from 1931 through 1934, following extensive windthrow from a storm during the spring of 1931. The slowly dying, uprooted and broken trees provided an excellent opportunity for the beetles to increase and attack green, standing trees. The beetles were again epidemic during 1941-'42, 1952-'53 and 1959 to the present (Meyer 1959).

Dense reproduction also developed as an understory in mature stands that had been partially or lightly thinned (Fig. 4). It also reclaimed fields that had been cleared by the settlers. I saw fields in 1933 and 1934 that were seeded to dense, even-aged reproduction.

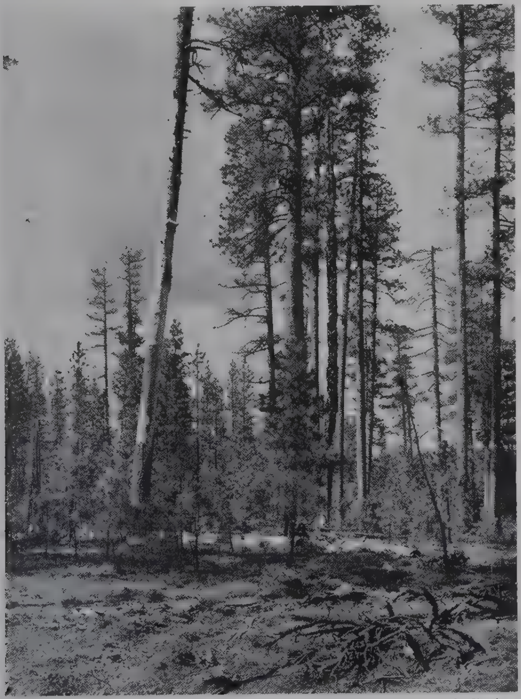

Fig. 4. Typical condition in southern portion of Cedar Valley. Overstory pines are gradually dying from pine beetle attacks. Understory competition is definitely a cause of lessened vigor and of deterioration of the overstory.

The younger age classes of reproduction are almost universal on areas not already occupied by the stands of large size poles. The valley area is approximately equally divided between the pole stands and the younger age classes.

In general the younger age classes are not growing as rapidly as the pole stands and growth over extensive areas has been quite slow because of intense competition. These stands are also competing intensely with the overstory pines and are reducing growth rate of these trees (Van Sickle & Hickman 1959). This renders the larger trees susceptible to beetle attack and encourages continuing epidemic attacks (Fig. 4).

Higher elevations and north slopes are being monopolized by true fir reproduction. On some areas dense fir pole stands 70 years old are competing with overstory pines. These stands occupy moister sites and it is probable that heavy early day grazing prevented fires from spreading readily over the forest floor. Also, since these areas were more remote from the settlers, there probably was less chance of them being purposely fired.

Fire hazard has increased greatly in the dense young pine and fir stands, which are interspersed with partly decayed, highly resinous snags and windfalls of dead trees.

Timber sale activity under Bureau of Indian Affairs regulations was initiated in 1952. Thus far about half of the valley has been selectively logged. The cut has taken approximately 50% of the merchantable stand, including decadent and high risk trees, leaving a reserve stand averaging 3500 to 4000 bd ft per acre of trees over 10 in. dbh. Thus it appears that the butterflies and pine beetles harvested about 8,000 bd ft per acre, approximately half of the original stand found by the white men, while, of the remaining stand, half has been harvested by the loggers, on an average stand per acre basis. Logging is presently being directed into areas of heavy beetle activity.

Discussion

In Cedar Valley there is evidence in the present well stocked ponderosa pine pole stands that fire thinned extensively when most stands were less than 13 years old and dominants had diameters at ground line of 0.5-1.5 in., as indicated by fire scar evidence. The heavy fuel burned consisted principally of butterfly and beetle killed pines. Other ground fuel was scanty because of frequent fires that had swept over the ground and early day overgrazing by domestic stock.

Most of these fire-thinned pole stands still appear comparatively open, with a pinegrass ground cover. Because of uninterrupted fuel accumulation of the past 40 to 50 years over much of this area, however, wild fires would now burn with considerable heat.

Fire thinning is patchy and most of the pole groups have developed to such size that competition between trees is again becoming acute. Unless foresters can relieve this overstocked condition by thinning it is believed by forest entomologists, from experience in other similar stands, that there will ensue epidemic attacks of the mountain pine beetle (*Dendroctonus monticolae*), or the Oregon engraver beetle (*Ips oregoni*).

The younger age classes are so dense that there does not appear much hope of useful growth unless they can be thinned. Because of many years of fuel accumulation any fire burning in these stands is apt to be severe. In critical fire weather it is apt to be devastating. On the Klamath Reservation in southern Oregon a fire in early September 1959 destroyed almost 15,000 acres of forest in one afternoon. This fire burned through dense pine reproduction and brush stands (Weaver 1960). It is my opinion that such fires will continue despite technological advances in fire prevention, detection and suppression.

These dense young stands will intensify in competition with the valuable over-story trees. The larger trees will continue to succumb to pine beetle attacks and their dead snag and windfall remains will add to already excessive fuel. Danger of devastating fires will increase.

SUMMARY

During the past century the ponderosa pine forest of Cedar Valley in southern Washington has experienced profound ecological changes. There remain only scattered, patchy remnants of the original magnificent, parklike forest. The valley is now almost universally characterized by dense stands of young pine and true fir. Pole sized stands of pine that originated about 1900 have grown well. Younger age classes, however, are so densely stocked that they are growing poorly. Through competition for limited soil moisture, these young trees adversely affect the growth rate of the remnant mature overstory. This encourages continuing epidemic beetle attacks on these high value trees. Fire hazard has greatly increased. These changes, which typify similar ones throughout the Ponderosa Pine Region, are the result of over-grazing by stock and attempts at total fire exclusion.

That frequent, periodic surface fires were important in the primeval pine forest is indicated by stand structure, species composition and the tree-ring and fire-scar record. Extensive even-aged stands originated after epidemic insect attacks that were followed by fires.

Interruption of nature's cyclic process was first caused by severe over-grazing of the pinegrass forest floor. This followed introduction of great bands of sheep and of homesteaders domestic stock in the 1880's. The settlers also cut timber for sawmills and cleared for agriculture. Severe climatic conditions were not conducive to farming and most of the settlers left after 1910.

From 1893-1895 inclusive, the forest was defoliated by a great epidemic of the pine butterfly. This was immediately followed by epidemic attacks of the western pine beetle, which was encouraged by the weakened condition of the defoliated trees. The butterfly-pine beetle attacks resulted in destruction of almost one billion board feet of pine sawtimber.

Seeds from the slowly dying trees germinated in a mineral soil seed bed on the stock trampled forest floor. This resulted in millions of pine seedlings, most of which became established about 1900. It is significant that this even-aged reproduction stand was thinned by fires set by stockmen and settlers in the early 1900's. The dominant or more fortunately situated individuals survived these fires and on release from competition made greatly accelerated growth. These trees are the well stocked large pole sized stands of Cedar Valley.

Following windthrow and continuing pine beetle infestation during the 1930, 1940 and 1950 decades, the remainder of the valley seeded in to younger age classes of reproduction. These stands are dense and make up an almost universal thicket under the remnant overstory of mature trees. It is significant that but minor portions of these stands have been subjected to fire as a result of organized fire suppression following 1910.

Normal growth in these stands will not occur until they are thinned. In the meantime competition for soil moisture will become more intense and conditions for devastating insect attacks and fires will increase.

REFERENCES

Clark, D. H. 1954. Butterflies invaded Cedar Valley. Spokesman-Review Inland Empire Magazine, Spokane, Wash., Jan. 24.

Cooper, C. F. 1960. Changes in vegetation, structure, and growth of Southwestern pine forests since white settlement. Ecological Monog. **38**: 129-164.

Keen, F. P. 1952. Insect enemies of western forests. USDA Misc. Pub. **273**, Govt. Print. Off.

Meyer, D. 1959. A study of forest infestation on the Yakima forest, Yakima Indian Agency. B.I.A. Rep. Apr. 18.

Neibel, Paul M. 1953. Plaintiff's brief in proceedings under interlocutary decree—The Yakima Tribe of Indians v. The United States, defendant.

Relander, C., Davidson, F. A., LeCrone, D. E., and Delany, R. 1955. The Yakimas' Treaty Centennial 1855-1955. The Republic Press. Yakima, Wash.

Saxton, J. B. 1914. Forest report for Yakima Indian Reservation. B.I.A. report by Deputy Supervisor of Forests.

Van Sickle, F. S. and R. D. Hickman. 1959. The effect of understory competition on the growth rate of ponderosa pine in north central Oregon. J. Forestry **57**: 852-853.

Weaver, Harold. 1943. Fire as an ecological and silvicultural factor in the ponderosa pine region of the Pacific slope. J. Forestry **41**: 7-15.

———. 1951. Fire as an ecological factor in the southwestern ponderosa pine forests. J. Forestry **49**: 93-98.

———. 1955. Fire as an enemy, friend and tool in forest management. J. Forestry **53**: 499-504.

———. 1958. Effects of burning on range and forage values in the ponderosa pine forest. Proc. Soc. of Amer. For. Salt Lake City, Utah. 212-214.

———. 1960. Implications of the Klamath fires of September, 1959, J. Forestry for pub.

THE LEVEL-OF-INTEGRATION CONCEPT AND ECOLOGY

J. S. Rowe
Forest Research Division, Department of Forestry, Ottawa

INTRODUCTION

Since at least the time of Comte the idea of arranging and classifying the sciences in an hierarchy according to level of inclusiveness or level of integration of subject matter has been common currency. That this notion has particular appeal in biological circles is evidenced by its widespread invocation whenever justification for a particular field of study or a scientific viewpoint is sought (for recent examples, see Egler 1942, Novikoff 1945, Sears 1949, Dice 1955, Mayr 1955, Miller 1957, Bray 1958, Muller 1958, Decker 1959, Odum 1959, Wright 1959). This article attempts to show how the idea may further illuminate both subject matter and point of view associated with *ecology*. It is also a commentary on the article by Major (1958), "Plant Ecology as a Branch of Botany," wherein he invited active discussion of relationships between plant geography and ecology.

CONCEPT OF INTEGRATIVE LEVELS OF ORGANIZATION

An article by von Bertalanffy (1950) pointed up some of the implications of the independent evolution of similar general conceptions and viewpoints in the various branches of science, with reference to organization of the latter in an hierarchy. He stated (p. 164), "Reality, in the modern conception, appears as a tremendous hierarchical order of organized entities, leading in a superposition of many levels, from physical and chemical to biological and sociological systems. Unity of Science is granted, not by a utopian reduction of all sciences to physics and chemistry, but by the structural uniformities of the different levels of reality." Thus, the structural similarities and logical homologies of the many different subordinate and superordinate systems make possible the formulation and deduction of principles valid for systems in general, giving rise to a new basic scientific discipline: General System Theory.

Feibleman (1954) has attempted to systematize some of the structural uniformities and inter-relationships of the integrative levels. His "Laws of the Levels" are worth close examination; they illuminate some aspects of mechanism, vitalism and teleology, and show the value of the integrative-levels concept as a positive aid to scientific research, pointing out that the understanding of an organization at any level requires attention also to the levels above and below. However, the thought occurs that careful attention ought to be given to that which is organized at the various levels. What exactly are the integrative levels to be? Obviously there must be some logical relationships if the hierarchy is not to be misleading and a source of confusion.

That there are differences of opinion as to how the different levels of organization are constituted, and inconsistencies within many of the proposed heirarchies of levels, is apparent from the following examples. Egler (1942) discussed 5 levels of emergent "organisms" (organizations or systems) in which plants predominate. From the simpler to the more complex these are: individual organisms, plant communities, biotic communities, vegetation and ecosystems. Clearly "vegetation" has a different conceptual status from either "biotic communities" or "ecosystems," and there are other inconsistencies of which Egler was doubtless aware when he wrote (p. 247) that "these emergent organisms are artificially isolated from the rest of nature for purposes of study, and . . . they may be arranged in different and equally satisfactory sequences for other purposes." Novikoff (1945) listed cells, tissues, organs, organ-systems, organisms and populations in increasingly higher levels of biological integration, and Odum (1959) in a similar sequence added, above populations, communities, ecosystems and the biosphere. Mayr (1955) carried the organization levels from cells, tissues, organs and individual organisms to populations and species, while Wright (1959) suggested the gene as autonomous at the level below the cell, and demes (interbreeding populations), species, ecologic systems and world fauna and flora at successive levels above the individual organism. Note the use of taxonomic categories as levels of integration, introducing a quite different mode of abstraction in the hierarchy. According to Bray (1958) most botanists and zoologists would place the "community" as the highest level of biological emergence, although "community" has been strongly criticized by some (e.g., Muller 1958) as referring to no consistent object. Returning for a second look at Bertalanffy's (1950) statement that "Reality, in the modern conception, appears as a tremendous hierarchical order of organized entities . . ." we are justified in asking: "What reality?" and "What organized entities?" These related questions lead to a consideration of the nature of empirical knowledge.

PERCEPTION AND OBJECTS OF STUDY

The natural sciences are concerned with empirical knowledge of nature, i.e., with what we perceive through the senses. Perception is not simply the registry by a receptive mind of what lies "out there"; rather it is an active intellectual process which provides consciousness with "objects" as vehicles of meaning for the world as sensed. Woodger (1929) has given a satisfying exposition of the relationship of perceived objects to the realm of nature and to the percipient; his theory of empirical knowledge is the basis from which the following argument has been developed.

The objects that we perceive—e.g., a house, a plant, a piece of soil—are basically volumes discriminated from their surroundings in space and time. On analysis they are observed to have structurally joined parts which strengthens our apprehension of their "objectness." On the other hand, we intuitively reduce to the status of an aggregate that in which we detect a lack of structural connection between what were first assumed to be "parts." The forest stand (vegetation community) appears from a distance to be a good solid object, but on close inspection it disintegrates into an aggregate of spatially separated trees and undergrowth plants. True there may be limited interconnections by root grafts, by epiphytism and parasitism, but community members have no *necessary* structural bonding; the unity of the community is in common occupancy of area. Still further removed from the structurally integrated object is the purely intellectual class entity such as the *species,* members of which may be widely separated in time as well as in space.

The distinction between the structurally integrated object (e.g., plant), the areal or geographic aggregate (e.g., plant community) and the non-object, non-aggregate class (e.g., species) is important in the problem of setting up a consistent level-of-integration scheme. The thesis here advanced is that each level must be an "object" as defined above, and that objects at successive levels must be structurally related. This can be illustrated by consideration of the organism, the organ and the cell, three objects whose status as integrative levels seems generally agreed upon. The organism contains the organ which contains the cell, and the cell is a structural part of the organ as the latter is a structural part of the organism.

We are now ready to state the basic propositions for a logical, useful level-of-integration scheme: The object of study of whatever level must contain, volumetrically and structurally, the objects of the lower levels, and must therefore be itself a part of the levels above. Each object will then constitute the immediate environment of the object at the level below while forming a structural-functional part of the object at the level above.

What objective level of organization stands above that of organism? According to the propositions just stated the enveloping object is the volumetrically inclusive, internally structured ecosystem (Fig. 1).

Each successive integrative level is not formed by aggregation of only one kind of lower level organization; the relationship between successive levels is not symmetrical. The object at each level is heterogeneous; it organizes a variety of spatially associated lower systems. The organ is more than cells, it is also connective tissue and other cell products; the organism is more than or-

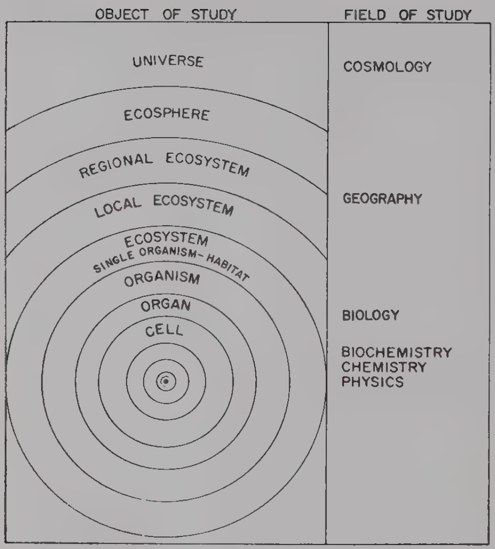

Fig. 1. Diagrammatic representation of objects of study at increasingly inclusive levels of organization; some corresponding fields of study are also shown.

gans, it is also their non-organ matrix of tissues, etc. So the object at the supra-organism level is more than a group of juxtaposed organisms or a group related reproductively; it is this group or community *plus* whatever else accompanies, interpenetrates and ties it together structurally, i.e., the land below, the air above.

A number of entities proposed as bona fide members of the levels-of-organization hierarchy come into question. The "organ-system," for example, fails when tested as the milieu of the level below, for it is not the environment of its member organs. "Organ-system" is a category which brings together by abstraction various spatially separate parts whose relationship consists in a certain cooperative outcome at the supra-organ (organism) level. Similarly "vegetation" is neither the environment of individual plants nor a structural organization of the ecosystem. "Deme," "population," "species," "flora"—all highly abstract taxonomic categories—must likewise be rejected as first order objects of study.

The Ecosystem as an Integrative Level

It has been pointed out by many that the term "ecosystem" has only categorical meaning (Sjörs 1955, Evans 1956, Friederichs 1958). This is implied too in Lindeman's (1942) inclusive definition of ecosystem as "any system composed of physical, chemical and biological processes active within a space-time unit of any magnitude." Tansley (1935) recognized that size and extent of ecosystems will be determined according to the purposes and methods of particular studies. Hills (1958) has referred to ecosystems ("forest sites") as wholes isolated from the continua in which they occur for purposes of evaluating their potential for production.

Recognition of the pragmatic element in the definition of ecosystems is a healthy reminder that there may be merit in various approaches to their selection. Some ecosystem units are practically "given" as self-evident objects, e.g., the limnologist's unit, the pond or lake. The terrestrial ecosystem is not always presented in so neat a package; usually it must be carved out of the living landscape by the use of appropriate criteria. To some people this subjectivity of boundary delineation is a stumbling block to acceptance of the ecosystem as an object of study, yet it need not be. A precise analogy is with soils, which have been made objects of scientific study despite the fact that their boundaries are fixed only by definition. Obviously study can be focussed on geographic "cores" though boundaries around them are elastic.

The criteria by means of which ecosystems can be defined and bounded are many. More important to the present discussion of the level-of-integration scheme is the fact that each ecosystem, encapsulating successively smaller ones down to the level of the individual organism-habitat cell or "monocene" of Friederichs (1958), is also part of an increasingly larger series. Thus above the level of organism extends a hierarchy of increasingly inclusive ecosystems, building from the local to the regional and on to the ultimate culmination in the all-encompassing world ecosystem or ecosphere, as Cole (1958) has called it.

The Ecosystem as a Geographic Object

Any single perceptible ecosystem is a topographic unit, a volume of land and air plus organic contents extended areally over a particular part of the earth's surface for a certain time. To some degree, therefore, it is unique in space as in time, for geography like history does not repeat itself. Study of the ecosystem is essentially topological, and the root *topos*, meaning "place," appears in many of the terms devised to describe its composition. Figure 2 shows the components of the biogeocoenosis, an ecosystem unit bounded with reference to a defined phytocoenosis (Sukachev 1954).

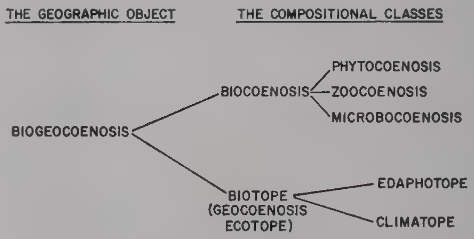

Fig. 2. Compositional components of the biogeocoenosis (an ecosystem comprehending a phytocoenosis) according to Sukachev.

As earlier emphasized in discussion of the level-of-integration scheme, a clear distinction needs to be maintained between the compositional categories and structural parts of objects. A simple ecosystem such as a "pine forest sand dune" can be analyzed into various structural parts: 1) into individual "cells," each consisting of one tree with its immediately surrounding air-soil volume, or 2) if there is an evident horizontally extended structure, into spatial units or volumetric landscape elements such as are centered on groups of trees, or 3) into structural-functional layers such as may be delineated by certain strata of the soil (Nikiforoff 1959) or strata of the atmosphere. Sukachev (1954) has designated the horizontal layers of the ecosystem "biogeocoenotic synusiae."

It is surprising that our vocabulary is inadequate for concise description of the ecosystem synusiae. The volume underfoot in which plants are rooted is commonly designated "soil" and studied as a whole and by horizons in pedology, but there is no comparable term nor field of study for the above-ground volume in which the shoots and crowns of trees and plants are likewise "rooted." We are aware of the contents of the air layer, but its own substantiality and stratification of composition, density, temperature, turbidity, etc., have largely escaped our attention, except where reciprocal influences on the forms of plants have been observed.. Topoclimatology, as defined by Thornthwaite (1953), is perhaps concerned more than any other branch of science with this layer or synusia, but none has treated it *in toto* as an object of study equivalent in importance to the soil stratum.

Relationship of Phytocoenosis to Ecosystem

Within the framework of the preceding sections, the status of the phytocoenosis or plant community can now be assessed. The phytocoenosis is an aggregate, a grouping based on area. But the object that occupies area at the level above the individual organism is the ecosystem, and logically the phytocoenosis is seen as a botanical component of ecosystem. It is a compositional category, not a unified structural part, and its status has neither the objectivity of its component individual plants nor of the ecosystem from which it is abstracted. The same can be said for other components similarly separated from the ecosystem on the basis of compositional class rather than structure. However, the soil body has a substantiality not shared by the phytocoenosis or zoocoenosis, for it is a volumetric whole, a clearly defined structural-functional layer. Soils might themselves be considered ecosystems, but recognition of their close dependence on the stratum above suggests their more logical treatment as ecosystem parts rather than as independent "natural bodies" (Crocker 1952).

Recognition of the basic difference between aggregate and structured object illuminates many problems which arise in the attempt to make communities and populations first-order objects of study. For example, some of the difficult and controversial subjects of "vegetation science" —e.g., competition, succession, productivity—are much simplified when examined at the level of the organism and at the level of the ecosystem.

Points of View in Scientific Study

Major (1958) continued the discussion by Egler (1942) of the "points of view" from which the subject matter of the various natural sciences can be studied. Both writers referred to Tschulok's (1910) presentation of 7 incommensurate material points of view applicable to the study of biological objects, these being taxonomy, morphology, physiology, ecology, chorology, chronology and genetics. Egler added "composition" to the list but dropped "genetics," considering the latter viewpoint to be covered by physiology, at least where individual organisms are the objects of study. Major reinstated genetics as "genesis," while accepting "composition" as a necessary auxiliary viewpoint. Despite the considerable attention they have attracted, the points of view do not seem to have been clearly defined in relation to "object of study" and to one another, nor integrated in a general theory of knowledge. In the following section the concept of integrative levels of organization will be shown to be relevant in providing a framework which gives specific and consistent meaning to a number of these viewpoints.

In Woodger's theory of knowledge previously referred to, the realities are strands of history or "events"; for example, the ontogeny of a frog is an "event," and the persistent stable phases—egg, larva, adult—we know as "objects." An object is what a slab of space-time is known as, and to our perception it is basically a volume, a form with related qualities. Thus the first viewpoint is morphology, the apprehension of physiognomy or form. Beyond perception of form, understanding is added in two ways. One mode of comprehension is analytical, looking within to the morphology of parts in their structural relationships (anatomy) and perhaps making an inventory of them (composition). The other mode of comprehension looks outward, seeing the object whole and searching for its relationships with the external world.

Now performance is the concomitant of form at all levels. What an object does continuously or repeatedly (its performance) is its function, and the antithesis between form and function rests simply on the artificial separation of space and time (Woodger, *op. cit.* p. 327). Concerned with study of function is the viewpoint physiology, the reference being primarily to the analysis of parts. Thus the question "How does the object function?" asks what are the performances of its parts in the service of the whole, while "What is its function?" asks what it does as a part of something more inclusive.

The outward looking viewpoint, concerned with study of the externally conditioned processes of an object, is ecology. Two different methodological approaches are usefully distinguished. First, the object may be maintained at the center of interest as a unity opposed to an unorganized, "factored" environment. Second, the object may be placed as a structural-functional part of more inclusive levels of organization, i.e., as an active constituent of a larger whole which directs its activity. In the latter sense, environment is conceived as itself an organized entity, and the realistic coenotic relationships with the object are implied.

The foregoing explains some of the differences of opinion surrounding definition of "ecology." Without reference to a level of integration scheme, ecology (at least behavioral or ethological ecology) is simply the study of the contingency of objects on abstract external factors, for example, the effects on a plant of impinging light, heat, moisture, nutrients. This is the basis on which Mason and Langenheim (1957) analyzed the meaning of *environment*. However, in the context of an hierarchy of organizations, ecology becomes study of the contingencies of objects at any level on the more inclusive levels of organization; for example, the ecology of a plant is its reaction to the ecosystem in which it participates, just as the ecology of an ecosystem is its relationship to the larger system which in turn surrounds it.

If the two modes of comprehension—the inward and the outward looking—are applied to the objects in an hierarchy of integrative levels, an overlapping of viewpoints must result. As we have seen, the physiology of an object looks to the functions of its parts, or to its function as a part, while the ecology of an object at any level seeks relationships to the more comprehensive world around it. So the ecology of a plant growing at a certain place coincides with some part of the physiology of the ecosystem which comprehends that place. The ecologist, working up through the hierarchy of organizations, at each level meets the physiologist working down.

As points of view that can be focussed on various objects or levels of organization, neither physiology nor ecology need imply a field of study. However there has been a tendency for physiologists to arrogate the individual organism as their field, calling the autecological aspects of their studies "environmental physiology." For example, the first experimental work on photoperiodism seems to have been pure ecology, though carried out by physiologists (Garner and Allard 1920). The ecologists, perhaps in self defense, have been making advances toward adoption of the ecosystem: "Ecology deals with all super-individual structures or organizations" (Dotterweich, *vide* Stocker 1956); "The ecosystem is the basic unit of ecology" (Evans 1956); "Ecology is the science of the super-individual complexes of nature" (Freiderichs 1958); "Ecology is the study of the structure and function of nature" (Odum 1959); "Ecology is the study of ecosystems" (Krajina 1960). Of course "ecology" has always denoted an inclusive subject matter in the English-speaking world, and inasmuch as study of the ecology of the organism demands attention to the physiology of the ecosystem, ecologists are perhaps justified in embracing this important study of process. Taking a leaf from the physiologists, the field might be called "functional ecology"! Billings (1957 p. 387) has of course used the precise phrase: "ecosystem physiology."

In addition to the relationships in form and function of wholes and parts, a number of viewpoints add meaning to an object in terms of position in space, development through time, and ties of class. Where an object is in space, relative to known points on the earth's surface, is its chorology. Establishment of the chorology of more than one object allows the formulation of spatial relations; for example, the detection of pattern in the distributions of individuals and populations. Note that such pattern of individual organisms is an element of structure though not total structure, at the ecosystem level above. Chorology elucidates ecology by showing where similar objects do and do not occur. Migration is chorologic change in time, and it is well to remember that individual plants rarely migrate, though the race or species does. The subject "geography" is discussed later, and it is enough here to note that a useful distinction can be drawn between chorology as the systematic viewpoint directed to the place in space of particular phenomena, and geography proper as study of "place" itself. Failure to distinguish between the viewpoint and the field of study is at the root of McMillan's (1956) argument that geographical study is a necessary preliminary to autecological investigations. I would say, rather, that chorology is one of a number of viewpoints that complements ecology, and that all viewpoints can profitably be applied to study of earth-place, the object of geographical investigation.

The viewpoint chronology traces the sequence of forms (and functions) culminating in a particular object. In philosophical terms, chronology describes an event, a strand of history, in terms of successive phases having sufficient endurance to be known as objects. From the standpoint of the terminal object, the chronology is called its ontogeny or genesis. The course it runs depends on both internal (physiological) and external (ecological) processes: it is both autogenic and allogenic. Given a regularity of internal and external conditions, chronology of similar objects (their ontogeny, development or "succession" of forms) can be expected to follow similar courses, i.e. chronology becomes predictable. Without this regularity in autogenic and allogenic factors, new objects appear in the sequence, and variation—often unpredictable—is recognized. This is evolution at the object level.

The relationship of objects according to likeness is classification, systematics. It is the striving for intellectual completeness that places classification as the synthesizing viewpoint, primarily based on morphology but drawing on all other viewpoints in order to establish, between phenomena, the maximum of relatedness in form and function, space and time. A distinction has to be made between the classification that is automatically and unconsciously done at the level of perception where what is sensed is identified as a particular object (tree, rabbit, etc.), and the conscious logical relating by kind that can be carried to elaborate lengths on the basis of selected criteria to yield morphologic, compositional, physiologic, ecologic, "geographic" and genetic classifications. Some implications are worth examining in detail.

Classes of objects can be arranged in time sequences to show presumed relationships; this constitutes phylogeny, chronology of the race or type. As Gilmour (1940) pointed out, the group or class of organisms is formed on the basis of correlation of attributes; it is prior to the phylogeny that can be derived from it. Thus classifications are phylogenetic by arrangement, after the classes have been organized on other grounds, and phylogeny must be considered derivative from systematics rather than the reverse. In one of its meanings, "history" is used to refer to the progenitors of an object far back in time, i.e., to racial evolution or phylogeny. It is clear that history in this meaning is speculative, non-inductive, describing a unique evolutionary succession on the basis of a taxonomy whose worth for this purpose is untestable. History as evolution of the race is by no means trivial, but dealing as it does with non-objects in explanatory rather than predictive ways (Scriven 1959) it is well to contrast it with development of the individual (ontogeny, morphogenesis) which *is* amenable to empirical study. It is also noteworthy that classification at analytic levels is basic to the viewpoint composition.

The foregoing treatment of the scientific points of view covers much the same ground as Major's (1958) article though with some differences of interpretation. A brief comparison will serve the purposes of summary.

Major begins with composition and structure, the latter viewpoint treated here as morphology and, by reduction, as anatomy. Thus structure is the inter-relation of parts (anatomy) as dominated by the character of the whole (morphology). In repeating Tschulok's definition of structure as "arrangement of these units of composition," Major placed the latter as a primary viewpoint. It seems more reasonable to me to reverse the priority, making composition subsidiary to structure because it is classificatory and "non-organic," yielding a quantitative inventory of parts at whatever level of analysis is desired; in short, it derives meaning from the structure it describes. Major's definition of the viewpoints physiology and ecology, looking to the processes within and the relationships without, are acceptable, as are the expressions of chorology as distribution in space and of classification as both summary and organization of knowledge. However, some confusion is introduced with the viewpoints genesis and history, the former treated as study of evolution and short-term change, the latter as long-term (palaeobotanic) change. It seems more reasonable to differentiate the chronology of objects (morphogenesis, and genetics in part) from their nonempirical evolutionary pasts (history or phylogeny), the latter viewpoint relying on classification.

All the viewpoints are inter-related through the objects on which they are focussed; they bring mutual support to scientific studies, particularly within a level-of-organization scheme (Fig. 3). Major's difficulties in setting forth a logical exposition of the scientific viewpoints largely stem from the impossibility of treating the community as analogous to the individual organism all down the line.

NATURE OF GEOGRAPHY

Space and time have entered the previous discussion in two ways: 1) as the necessary framework of perception and 2) as points of view—chorology and chronology—whereby particular phenomena are systematically placed

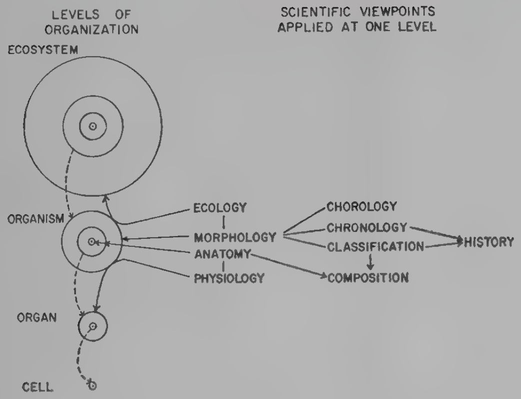

FIG. 3. Related objects (levels of organization), and scientific viewpoints as applied at one level. Note that the viewpoints, anatomy, composition and physiology are applied in descending the levels while morphology and ecology are applied in ascending.

in spatial and temporal relationships and sequences. In yet another aspect, that of geography and history, space and time provide the unifying background for phenomena that may not be systematically related.

Hartshorne (1939) in his stimulating monograph "The Nature of Geography" drew attention to the argument that 3 different approaches are available and necessary for the full comprehension of reality. The idea was proposed by the philosopher Kant (*vide* Hartshorne 1939) in an essay on geography, wherein he pointed out that we may "classify" our empirical knowledge according to conceptions (logical classification) or according to time and space (physical classification). Through the former we obtain a system of nature, a register of the whole; through the latter a geographical and historical description of nature. Description according to space (treating all phenomena of a region) is geography, that according to time (all phenomena of a period) is history. This last is "history" treated as subject rather than as viewpoint. Apparently influenced by Kant, Humboldt placed geography as the study of that which exists together in area, as opposed to the systematic sciences focussed on particular phenomena, and much later the German geographer Hettner independently formulated the same idea (Hartshorne 1958). The "object" of geographical study is therefore to be understood as earthspace and its contents, i.e., the complex juxtaposition of phenomena that gives character to region, locality, place. By this definition, "plant geography" is the topical study of plants associated in place, as characteristic of that place.

When geography and the systematic sciences are contrasted it is on the supposition that the object of geographic study is unique while that of the systematic sciences is not. Actually all phenomena are to some extent unique, but the more inclusive the level of organization, the more apparent the elements of uniqueness become. Thus the individuality of the organism stands out in comparison to that of the cell, while the individuality of the ecosystem (a geographic entity) is still more clearly evident. Quoting James (1954), "In the field of geography, as long as attention is focused exclusively on the difference between places, the unique quality of each place is emphasized, and for some purposes this is exactly what should be done. However, likenesses between places may also be important, and for some purposes more important than the differences. The identification of the similarities between places is a geographic method of arriving at a generalization . . . of the characteristics of area." This means that geographic entities are amenable to systematic study; it is only necessary to concentrate on their repetitive characteristics. Although classifiability of subject matter is a prominent characteristic of the systematic sciences, and uniqueness to which only description is fully adequate the mark of geography, the separation of the two is merely a matter of degree. The differences are certainly not of the fundamental kind that sets history apart from both in the different dimension of time.

ECOSYSTEM AND POINTS OF VIEW

The ecosystem as here used is a geographic object, and the relevance of the points of view to geographic study can be illustrated with it. At the same time, some questions concerning the suitability of the ecosystem as an object of biological research may be answered.

From the viewpoint morphology, a terrestrial ecosystem is a volume of earth space with organic contents, separated from its neighbors by reasonable divisions in the empirical continua of biota, soil, physiography. It resembles a model formed by a slab of clear plastic (atmosphere) bound to a porous slab of metal (lithosphere) by wooden dowels (the plants and other organisms). Horizontal or vertical slices through it reveal the anatomical structure, hitherto dissected in bits and pieces by the microclimatologist, the botanist, the pedologist and the geomorphologist working separately. An inventory of the parts, sorted into classes, is given by the viewpoint composition. The physiological viewpoint is directed to internal functions: the production and cycling of materials in and between the anatomical parts, the accumulation of matter and energy in the whole. The ecology of the ecosystem is its relationships to the larger enveloping geographic system of which it is a part and with which it continuously exchanges materials and energy. From the chorologic viewpoint, ecosystems are mapped in their positions at the earth's surface. Chronology records the character of sequent ecosystems at one particular place, and the genesis of a particular one by "succession" refers to the observable changes that come about through time in a fixed space. Such changes are both internally and externally conditioned (autogenic and allogenic), and given some regularity in both physiological and ecological processes, the chronology may run at least a predictable short-term course. Ecosystems can be classified according to similarities in form, structure and composition, with support from the other viewpoints. It needs to be stressed that the ecosystem is not just an amplified phytocoenosis; typology must therefore be based on more than botanical composition (Rowe 1960). Finally, history seeks to trace in generalities and for particular places the climatic and geomorphologic changes of the past, as well as the evolution and migration of organisms, leading up to the syntheses of contemporary ecosystems.

In dealing with such patterned, intergrading objects as soils and ecosystems there is a necessary close reciprocity between the definition of units and classification. The class concepts formed in one area will be used in another to divide a continuum into reasonable segments. Thus classification is more than systematization of what is already given; it is a means of "catching the rabbit."

VEGETATION AND THE POINTS OF VIEW

It has been shown how objects in an hierarchical level-of-integration scheme are amenable to scientific study by a number of incommensurate viewpoints. These same viewpoints can be focussed on presumed objects of study and used to detect those that are specious. As the status of the plant community as a first-order object of investigation has been questioned, it will now be tested by the scientific viewpoints.

The community is an aggregate of objects whose primary bond is common occupancy of area. This areal basis confers a degree of apparent substantiality on the community, for once the area is bounded a spatial unit appears. Furthermore the non-structural viewpoints chorology (position in space), chronology (succession), classification and composition are perfectly applicable to the areal community, as they are to many other non-objects. It might be noted that even the flora, whose abstract status will be granted without argument by most, can be mapped in space, chronicled in time, dissected into compositional categories and classified on paper. It is significant that vegetation is more commonly mapped, and classified according to composition, than studied.

Difficulties are encountered when the community unit is subjected to the viewpoint morphology, for immediately one perceives that both outward form and inner structure lack articulation. The idea of structure in vegetation takes certain liberties with what is perceived; the eye skips from plant to plant across the intervening spaces, searching out the repetitive growth forms which are then used to delineate a diffuse physiognomy.

Without structural form, the basis for performance is lacking; hence the difficulties of applying the viewpoint physiology in vegetation. Individual plants have their functions; not so the community. Major's statement (op. cit. p. 357) "there is a physiology of vegetation expressible by water and CO_2 relations of plant communities *considered in their ecosystems . . .*" (my italics) touches the important point; the reality is a physiology of the ecosystem, in which plants function. Again, the ecological viewpoint cannot apply in any clear way to the stand of vegetation. Becking (1957 p. 467) defines synecology as "study of the inter-relations between a plant community and its environment." But can a community be said to have an environment as separate from the environment of its members unless it is considered to be a volumetric object, ie., an ecosystem?

Discussion

There are signs that students of community biology are not entirely satisfied with the present basis of their subject. For example, Bray (1958) pointed to a neglect of structure analysis in the study of communities, while Miller (1957) noted that "community ecology has been particularly slow to progress from the study of structure to that of function." Contemporary books on quantitative ecology (Greig-Smith 1957, MacFadyen 1957) stress the importance of community structure, while in fact dealing primarily with mathematical analysis of composition, growth and population pattern. Shift in attention from community to the ecosystem which comprehends it could give deeper meaning to structure and function by providing the operational framework.

The argument does not imply that the community concept is valueless; the aim is to set the community in its logical place within the purview of science, thus avoiding the difficulties inherent in its treatment as an object of study of the same status as individual organism and ecosystem. Its limitations being recognized, the community remains a useful though limited subject of study. Also, like the concept *species*, it can serve the purpose of summarizing and classifying knowledge gained at more objective levels. For example, the "vegetation stand" or "community of plants" is a useful envelope in which to file information concerned specifically with plants juxtaposed in particular areas, such information having been gained by the objective study of the individual plants and of the ecosystems in which the plants are functional parts. Again, there can be no doubt that, as a topical aspect of geography, the description and mapping of vegetation has proven uses. In short, plant sociology serves its own purposes admirably, but for many other purposes, e.g., as the basis for study of problems of productivity and land management, it is inadequate.

It is of interest that the individualistic nature of the phytocoenose or vegetation community can be deduced from its relationship to the geographic ecosystem. While Gleason's (1927) argument for the "individualistic concept" of the association was not derived in this way, it did stem from sound geographic and historical considerations, and he was fully aware of the uniqueness that position in earthly space and in time imply. The controversial point of the "individualistic concept" has been the implication by many of its champions and opponents that its acceptance rules out the possibilities of classification. This, however, is a misconception of the nature of classification. There is no antithesis between individualism and classification so long as purpose finds *some* similarities in the units defined. Ecosystems, soils, phytocoenoses, even organisms, all are individualistic but none the less all are classifiable.

Summary

The concept of the integrative levels of organization is an illuminating one in the field of biological research. It can be a source of confusion, however, if entities of different orders of abstraction are built into the hierarchy. From a theory of empirical knowledge which is derived from Woodger (1929), a basis for relating the objects of study at successive levels according to the principle of spatial inclusiveness and structural relatedness is presented. The object of each level is seen as the environment of the objects at the levels below and as a specific structural-functional part of the object at the level above.

The ecosystem, a geographic life-filled space, is the object of study at the level above the organism. It is divisible into structural parts, vertically or horizontally, or into class parts (components) such as plants, animals, climatic and soil environment. Thus the status of the stand of vegetation (phytocoenose) is clarified; it is the abstract botanical component of a volume of earthly space (the ecosystem) which stands as the primary object of research.

Six primary viewpoints and three derivative ones are shown to encompass adequately the study of an object. As a form in space it is studied by *morphology*, and analytically by *anatomy*. A quantified catalogue of its classified parts is given by the viewpoint *composition*. Relating the object as a percept to inner and outer phenomena are the viewpoints *physiology* and *ecology*, respectively. Relating the object systematically to other phenomena in space, in time and by kind are the viewpoints *chorology*, *chronology* and *classification*. *History* traces past evolution deductively, by means of reasonable classification and circumstantial evidence. Within an objective, integrative level-of-organization scheme, the viewpoints physiology and ecology are shown to overlap where objects at adjoining levels are studied. Thus, for example, the physiology of an ecosystem coincides in part with the ecologies of the constituent organisms.

The ecosystem can be examined from all the viewpoints even though it is a geographic (i.e., unique) entity. However, the application of the points of view to vegeta-

tion as subject matter shows the limitations of the latter as an object of study. It is concluded that parallel concepts such as *population* and *community* also lack the substantial form and structure that confer first order objectivity, hence these too qualify for scientific study only as phenomena of lesser status than individual organism and ecosystem. Classifiability is, however, unaffected by the conceptual status of these entities.

REFERENCES

Becking, R. W. 1957. The Zürich-Montpellier school of phytosociology. Bot. Rev. **23:** 411-488.

Bertalanffy, L. von. 1950. An outline of general system theory. British J. for the Philosophy of Sci. **1:** 134-165.

Billings, W. D. 1957. Physiological ecology. Ann. Rev. Plant Phys. **8:** 375-392.

Bray, J. R. 1958. Notes toward an ecologic theory. Ecology **39:** 770-776.

Cole, L. C. 1958. The ecosphere. Scientific American **198:** 83-92.

Crocker, R. L. 1952. Soil genesis and the pedogenic factors. Quart. Rev. of Biol. **27:** 139-168.

Decker, J. P. 1959. A system for analysis of forest succession. Forest Science **5:** 154-157.

Dice, L. R. 1955. What is ecology? Scientific Monthly **80:** 346-351.

Egler, F. E. 1942. Vegetation as an object of study. Philosophy of Science **9:** 245-260.

Evans, F. C. 1956. Ecosystem as the basic unit in ecology. Science **123(3208):** 1127-28.

Feibleman, J. K. 1954. Theory of integrative levels. British J. for the Philosophy of Sci. **5:** 59-66.

Friederichs, K. 1958. A definition of ecology and some thoughts about basic concepts. Ecology **39:** 154-159.

Garner, W. W. and H. A. Allard. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction of plants. Jour. Agric. Res. **18:** 553-606.

Gilmour, J. S. L. 1940. Taxonomy and philosophy. In "The New Systematics." p. 461-474. ed. Julian Huxley, Oxford, Clarendon Press.

Gleason, H. A. 1927. Further views on the succession-concept. Ecology **8:** 299-326.

Greig-Smith, P. 1957. Quantitative plant ecology. Butterworth's Scientific Publications. London.

Hartshorne, R. 1939. The nature of geography. Annals Assoc. Amer. Geogr. Vol. **29** (3 & 4).

Hartshorne, R. 1958. The concept of geography as a science of space, from Kant and Humboldt to Hettner. Annals Assoc. Amer. Geogr. **48:** 97-108.

Hills, G. A. 1958. Soil-forest relationships in the site regions of Ontario. Proc. First North American Forrest Soils Conference. p. 190-212. Mich. State Univ., East Lansing, Mich.

James, P. E. 1954. The field of geography. American Geography—Inventory and Prospect. (Chap. I) Assoc. Amer. Geographers. Syracuse Univ. Press.

Krajina, V. 1960. Ecosystem classification of forests. Silva Fennica **105:** 107-110.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23:** 399-418.

MacFadyen, A. 1957. Animal Ecology. Sir Isaac Pitman & Sons, Ltd. London.

Major, J. 1958. Plant ecology as a branch of botany. Ecology **39:** 352-363.

Mason, H. L. and J. H. Langenheim. 1957. Language analysis and the concept *Environment.* Ecology **38:** 325-340.

Mayr, E. 1955. Summation: Systematics and modes of speciation. Biology Colloquium. Corvallis.

McMillan, C. 1956. The status of plant ecology and plant geography. Ecology **37:** 600-602.

Miller, R. S. 1957. Observations on the status of ecology. Ecology **38:** 352-354.

Muller, C. H. 1958. Science and philosophy of the community concept. American Scientist **46:** 294-308.

Nikiforoff, C. C. 1959. Reappraisal of the soil. Sci. **129 (3343):** 186-196.

Novikoff, A. B. 1945. The concept of integrative levels and biology. Sci. **101:** 209-215.

Odum, E. P. 1959. Fundamentals of ecology. 2nd ed. W. B. Saunders Co., Philadelphia.

Rowe, J. S. 1960. Can we find a common platform for the different schools of forest type classification? Silva Fennica **105:** 82-88.

Scriven, M. 1959. Explanation and prediction in evolutionary theory. Science **130(3374):** 477-482.

Sears, P. B. 1949. Integration at the community level. American Scientist **37:** 235-243.

Sjörs, H. 1955. Remarks on ecosystems. Svensk Botanisk Tidskrift **49:** 155-169.

Stocker, O. 1957. Grundlagen, Methoden und Probleme der Ökologie. Berichte Deutschen Botanischen Gesellschaft **70(9):** 411-423.

Sukachev, V. N. 1944. On the principles of genetic classification in biocoenology. Jour. of Genl. Biol. Zhurn. Obschch. Biologii) **5(4):** 213-227. English translation of full paper by F. C. Raney, MS only; edited and condensed by R. Daubermire in Ecology **39:** 364-367. 1958.

Sukachev, V. N. 1954. Die Grundlagen der Waldtypen. Festschrift für Aichinger **1:** 956-964.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology **16:** 284-307.

Thornthwaite, C. W. 1954. Topoclimatology. Proc. Toronto Meteorological Conference, A.M.S. and R.M.S., Sept. 9-15, 1953.

Woodger, J. H. 1929. Biological Principles, a critical study. Harcourt, Brace & Co. London & New York.

Wright, Sewall. 1959. Genetics and the hierarchy of biological sciences. Science **130(3381):** 959-965.

COMPETITION BETWEEN MAPLE-BASSWOOD AND FIR-SPRUCE COMMUNITIES IN ITASCA PARK, MINNESOTA

Murray F. Buell and William E. Martin
Department of Botany, Rutgers University; Department of Botany, University of Minnesota

Itasca Park, Minnesota, is in the broad transition between the fir-spruce (*Abies balsamea-Picea glauca*) forest region to the north and northeast and the sugar maple-basswood (*Acer saccharum-Tilia americana*) region to the west and southwest. Within this transition from deciduous to coniferous forest, both kinds of community appear to occur as climax. In 1938 Kell showed that the soils occupied by maple-basswood communities in Itasca Park have a somewhat higher moisture retaining capacity than those occupied by fir-spruce communities, but the difference was so slight that she considered both communities as having equal climax status. Also, both communities meet the following criteria for recognition as climax: ability to replace other upland communities, ability to resist invasion by other communities, and ability to perpetuate themselves after initial establishment.

In places where fir-spruce and maple-basswood communities occupy contiguous areas, the boundary between them may be very sharp. One such boundary located in Itasca Park along the Bohall Trail, which is west of Lake Itasca (NE, SW, S 10, T 143 N, R 36 W), is especially interesting because it is one of the areas where Kell made soil collections, and it has been observed rather carefully since 1939.

The evidence available in 1939 (Buell and Gordon 1945) indicated that the fir-spruce community was more aggressive than the maple-basswood. Islands of fir were found within the maple-basswood community. Maple-basswood reproduction and ground cover were absent under these islands of fir and stopped abruptly at the boundary between the two communities.

In subsequent years the islands of conifers in the deciduous forest underwent deterioration. By 1955 (Buell 1956), only a few scattered firs remained alive. Maple-basswood reproduction and ground cover were found in the fir island areas where they were absent in 1939.

By the summer of 1959, further conspicuous changes had become apparent. The main boundary between the two communities had shifted at the expense of the fir-spruce, and young islands of maple-basswood had become established in the fir-spruce community. These changes seem to represent a reversal of the situation which was extant 20 years ago. The present study was undertaken to measure these changes and to consider their possible cause and significance. Our nomenclature follows Gray's Manual of Botany, 8th edition (Fernald 1950).

Methods

The initial study of the boundary between fir-spruce and maple-basswood in 1939 involved the establishment of a 1 m × 5 m trenched plot with its long axis across the boundary line. At that time, maple-basswood reproduction stopped abruptly at the mid-point of the plot. Because the trenched plot was marked by permanent posts, it was possible, in 1959, to measure the distance that various species had moved into the conifer half of the plot. This was done not only in the original 1 m × 5 m plot but also, in order to discount the possible effect of trenching, in meter-wide strips on each side of the original plot.

A count of fir trees over 1 in. dbh was made within a 5 m radius from the conifer end of the original plot. Windthrows and trees which were dead but still standing were included in this tally to provide some measure of the degree of thinning of the conifer stand.

Permanent quadrats measuring 2 m × 5 m were established in the young maple-basswood islands within the fir-spruce community. Three sites were selected to represent the habitat extremes in an upland forest: (1) a low mesic area, (2) a dry slope, and (3) a swamp margin. In all three sites there were numerous logs of various sizes of spruce or fir or both on the ground. In addition to occasional conifers still standing in the openings, the first two areas had scattered aspen (*Populus tremuloides*); and in the third there were a few large balsam poplars (*Populus balsamifera*). Immediately above all three plots there was no canopy or else a canopy composed only of the thin crowns of a few aspens.

In each of the 2 m × 5 m quadrats the following data were collected: (1) Individuals of tree species were tallied in four size classes: less than 1 ft, 1-2 ft, 2-4 ft, and over 4 ft. (2) Terminal growth increments for the current season were measured and an average computed for each species. (3) Herb species were listed, and the relative abundance of each species was estimated as abundant, common, or rare.

Results

The results from the study of the 1939 boundary between maple-basswood and fir-spruce show that sugar maple reproduction had become well established throughout the conifer half of the original quadrat from which it had formerly been excluded. Sugar maple seedlings occurred over the entire plot, and some had reached a height of over 2 ft. The maple-basswood ground cover had also extended over the entire plot and over considerable areas adjacent to it. While 19 species had invaded the conifer half of the plot and adjacent areas, the density of this ground cover was still low. The estimated herbaceous cover on the hardwood half of the quadrats studied was 70% compared to 35% on the conifer half.

Within a radius of 5 m from the conifer end of the original quadrat there were only 14 living fir trees over 1 in. dbh but 49 dead ones. In the 1-3 in. size class there were 37 dead and 4 alive; in the 3-6 in. size class, 7 dead and 4 alive; and in the over 6 in. size class, 5 dead and 6 alive. Similar deterioration of the conifer stand was observed along the entire boundary between conifers and hardwoods. The invasion of this margin by maple-basswood reproduction and ground cover was also observed along the entire boundary.

The other three sites studied are all located within the coniferous forest. No. 1, the low mesic area, No. 2, the dry slope, and No. 3, the swamp margin are located approximately 165 ft, 195 ft, and 340 ft, respectively, from the boundary between the two communities. The data from these three young islands of hardwood reproduction and ground cover (Table I) show what appears to be an aggressive establishment of the maple-basswood community in the openings formed by windthrow in the conifer forest. It should be noted that all the quadrats were well stocked with hardwood reproduction while conifer reproduction is virtually absent.

Black ash (*Fraxinus nigra*) is not a typical member of either the maple-basswood or the fir-spruce communities, and the fact that its seedlings and saplings are more

Table I. Maple-basswood reproduction in three openings in the fir-spruce forest. Data are counts of individuals of four different height classes in one 2 m × 5 m quadrat in each opening (Nos. 1, mesic site; 2, dry site; and 3, swamp margin). The openings are described in the text

Species	<1 ft.			1-2 ft.			2-4 ft.			>4 ft.		
	1	2	3	1	2	3	1	2	3	1	2	3
Acer saccharum	3	13	1	3	10	1	6	13	1	0	2	8
Fraxinus nigra	5	15	10	4	6	27	0	2	30	0	0	2
Tilia americana	2	0	0	3	0	0	0	1	1			
Acer rubrum	0	3	0	2	1	2	1	0	1			
Ulmus americana	0	1	0	0	0	0	1	0	0			
Populus tremuloides	0	2	0	3	1	0	3	6	0			
Quercus borealis	0	2	0	1	0	1						
Pinus strobus	0	1	0									
Abies balsamea	0	4	3									
Quercus macrocarpa	0	1	0									

numerous than those of either sugar maple or basswood may be misleading unless it is also noted that sugar maple reproduction is significantly more abundant on the dry site and that black ash reproduction is concentrated on the swamp margin.

On the dry site, the average 1959 terminal growth increment (based on five measurements) for black ash was 2.0 in. and for sugar maple, 11.0 in. On the swamp margin, the average increment for black ash was increased to 8.0 in. and for sugar maple, to 13.8 in. While the averages for black ash are based on individuals 1-2 ft and 2-4 ft tall and those for sugar maple on individuals 2-4 ft and over 4 ft tall respectively, there remains a strong basis for the conclusion that both species grew more vigorously on the swamp margin than on the dry site and that sugar maple grew more vigorously than black ash on both sites. Perhaps the most significant feature of terminal growth measurements was that sugar maple saplings were tallest and growing more vigorously than any other species in the wettest of the three locations, the swamp margin.

Herbaceous species were also well established in the hardwood islands, where they formed a more or less continuous herb stratum which is a common feature of maple-basswood communities. The largest number of herbaceous species (21) was found at quadrat No. 1, nearest to the hardwood forest, and the fewest (17) at quadrat No. 3, farthest from the hardwood forest. The species of major importance in the plots in these hardwood islands were *Anemone quinquefolia, Asarum canadense, Aster macrophyllus, Carex pedunculata, C. pensylvanica, Cornus canadensis, Galium triflorum, Hepatica americana, Maianthemum canadense, Mitella nuda* and *Streptopus roseus* var. *longipes*. In addition to those species of major importance, i.e., those found to be abundant on one or more quadrats or to occur uniformly on all three quadrats, the following were found to be present on only one or two of the three quadrats: *Linnaea borealis* and *Amphicarpa bracteata* common on quadrat 1; *Sanicula marilandica* common on quadrat 2; *Athyrium felix-femina* var. *michauxii* common on quadrat 3; *Thalictrum dioicum* and *Oryzopsis asperifolia* sparse on quadrats 1 and 3; *Pyrola secunda* sparse on quadrats 1 and 2; *Trientalis borealis, Arisaema triphyllum,* and *Osmorrhiza claytoni* sparse on quadrats 2 and 3; *Luzula acuminata, Uvularia grandiflora, Lathyrus ochroleucus, Aquilegia canadensis,* and *Circaea alpina* sparse on quadrat 1; and *Fragaria vesca* sparse on quadrat 3.

Discussion

The manner in which a fir-spruce forest commonly perpetuates itself is of particular significance to this study. Fir is especially susceptible to windthrow and breakage so that small openings beset with a tangle of fallen trees are common features of fir-spruce forests. These openings are ordinarily filled by dense thickets of fir saplings (Cooper 1913, Buell and Niering 1957) which eventually, through growth and competition, replace the gap in the canopy. This kind of regeneration can be observed in the fir-spruce forest about 200 yards east of the study area. Also, spruce and fir seedlings and saplings are well established and hardwood species (except aspen) are virtually absent throughout an extensive wind-damaged area near the shore of Lake Itasca about 600 yards east of the study area. In the study area, where there is an abundant supply of seeds from both the coniferous and the deciduous trees, sugar maple and basswood are able to occupy the openings more rapidly than spruce and fir. The most vigorous growth of saplings of deciduous trees was found in the wettest of the openings studied.

Fire in the distant past (ca. 1810-15) and overpopulation of deer in the recent past (ca. 1935-45) have been important environmental factors in these forests, but it seems unlikely that the present trends at this forest ecotone are influenced by either. Since Kell's work showed that the fir-spruce forest was favored by a soil of somewhat lower moisture retaining capacity than that of the maple-basswood, one is tempted to believe that a dry-climate regime in this area might favor the fir-spruce forest while a wet-climate regime might favor the maple-basswood community. People who have worked in the Itasca area for some time have become well aware of conspicuous vegetation changes apparently related to the change from a dry period to a wet period. One such pronounced change has recently been recorded along with the accompanying climatic record (Isaak, Marshall and Buell 1959). Whether or not the cause of the changes indicated here is simply an increase in moisture or actually involves a more complex environmental change, what we are witnessing may be the delicate tipping of the balance between two forest climaxes where they come in contact.

References

Buell, M. F. 1956. Spruce-fir, maple-basswood competition in Itasca Park, Minnesota. Ecology **37**: 606.

——— **& W. E. Gordon.** 1945. Hardwood-conifer forest contact zone in Itasca Park, Minnesota. Am. Midl. Nat. **34**: 433-439.

——— **& W. A. Niering.** 1957. Fir-spruce-birch forest in northern Minnesota. Ecology **38**: 602-609.

Cooper, W. S. 1913. The climax forest of Isle Royale, Lake Superior, and its development. Bot. Gaz. **55**: 1-44, 115-140, 189-235.

Fernald, M. L. 1950. Gray's Manual of botany, 8th ed. American Book Company.

Isaak, Daniel, W. H. Marshall, and M. F. Buell. 1959. A record of reverse plant succession in a tamarack bog. Ecology **40**: 317-320.

Kell, Lucille L. 1938. The effect of moisture retaining capacity of soils on forest succession in Itasca Park, Minnesota. Am. Midl. Nat. **20**: 682-694.

GERMINATION OF CHERRYBARK AND NUTTAL OAK ACORNS FOLLOWING FLOODING[1]

C. B. Briscoe
Tropical Forest Research Center, U. S. Forest Service, Rio Piedras, P. R.

Frequency and duration of flooding is undoubtedly one of the most important environmental factors affecting species distribution in bottomland forests. In the life of a tree this influence is first exerted on the seed, and the capacity of seeds to retain viability after submergence by flood water may well be an important factor in determining the success of a species in a particular ecological niche.

Bare sandbars and mud flats are colonized by cottonwood (*Populus deltoides* Bartr.), willow (*Salix nigra* Marsh.), and sycamore (*Platanus occidentalis* L.).[2] Seeds blow onto these sites immediately after flood waters have receded or are stranded by the receding waters. These seeds will remain viable many days in water and will actually germinate under water (Hosner 1957, Briscoe and DuBarry 1959).

Areas almost continuously flooded typically support stands of bald-cypress (*Taxodium distichum* [L.] Rich.) and water tupelo (*Nyssa aquatica* L.). The seed of these species has shown no capacity to germinate under water, but their germination percentage does not drop to zero even after months of submersion (Demaree 1932, Shunk 1939, Briscoe 1959, Applequist 1959).

Two other physiographic sites common in the bottomlands are (1) wet flats and (2) well-drained flats or low ridges. A species typical of the former is Nuttall oak (*Quercus nuttallii* Palmer); cherrybark oak (*Q. falcata* var. *pagodaefolia* Ell.) is rare except on the latter. Acorns of these two species were submerged for various periods to determine whether their responses differed.

Procedure

Acorns previously kept 4 months in moist stratification at 33-35°F were counted in 100-seed lots and randomly assigned to treatments, 4 lots to each treatment indicated in Table I. The cherrybark oak acorns and one lot of Nuttall oak acorns were collected near Baton Rouge, Louisiana. The other two lots of Nuttall acorns were collected near Plaquemine, Louisiana, and near Stoneville, Mississippi. All submersion treatments were terminated on April 16, 1958, and were begun prior to that date by the length of treatment indicated.

In selecting the length of periods for submerging the acorns one week was adopted as the basic unit. It was judged to be longer than the normal period of flooding on well-drained sites yet common on the poorly drained areas. Because the study was exploratory, the second length of period was twice the first, and the third was twice the second; with the check, these called for flooding periods of 0, 1, 2, and 4 wks. For operational convenience, the actual periods used were 0, 8, 18, and 34 days.

As pointed out by Bergman (1920) flooding effects can be studied much more economically in ordinary tap water than in swamp water. Therefore, seeds were submerged in both types to determine whether the results were the same, and thus whether future studies need be made in the swamp.

Table I. Germination of cherrybark and Nuttall oak acorns following flooding treatments

Water	Days flooded	Germination Percentages	
		Cherrybark oak	Nuttall oak
None..........	0	43	39
Swamp........	8	42	45
	18	37	43
	34	24	40
Tap...........	8	44	44
	18	42	44
	34	26	42
Airless tap.....	8	43	
	18	38	
	34	28	
All waters......	8	44	41
	18	41	44
	34	26	42

Submersion of acorns in the assigned water was in bags of saran screening, except that airless treatments were in sealed bottles of tap water sunk intermixed with the corresponding bags.

The swamp water was in a natural slough in the first bottom of the Mississippi River, but outside the mainline levee. The water was not stagnant during the test period; it contained a great deal of suspended organic material but was not muddy. Tap water was in tanks of galvanized iron anchored in the slough. Temperature of both waters varied from 37° to 40°F during the experiment, but they did not vary from each other on any given date by as much as one degree.

All germination tests were in a steam-heated building, in wooden flats filled with vermiculite. Each test was terminated at the end of 10 successive days without germination.

Results

As indicated above, individual germination percentages shown in Table I are the mean of four 100-seed samples.

The combined analysis of variance, Table II, showed the Species x Days interaction to be highly significant, but no comparison involving type of water approached significance. Neither Species nor Days was significant when tested against the mean square of their interaction.

In order to make a more sensitive comparison between flooding periods, as well as to test the airless tap water results which could not be included in the combined analysis, results for each species were then analyzed separately.

For cherrybark oak the mean square attributable to type of water and to Water x Days interaction failed to approach significance, but differences among flooding periods were highly significant (variance ratio of 67.379). Further tests showed that the difference between 8 and

---

[1] The data on which this note is based were collected while the writer was Assistant Professor of Forestry, Louisiana State University.

[2] Additional tree species colonize such sites, but—to the writer's knowledge—no studies have been reported on whether their seeds germinate under water. *Tamarix pentandra* Pall. germinated floating on water (Horton et. al., 1960).

TABLE II. Combined-species analysis of variance

Variable	Degrees of Freedom	Sum of Squares	Mean Square	Variance Ratio$_1$	Variance Ratio$_2$
Species.......	1	4,302.10	4,302.10		3.008 NS
Days.........	2	6,009.29	3,004.64		2.101 NS
Species x Days.	2	2,859.97	1,429.98	12.423 HS	
Water........	1	157.69	157.69	1.370	
Water x Species	1	2.94	2.94	0.026	
Water x Days..	2	60.12	30.06	0.261	
Water x Species x Days....	2	143.62	71.81	0.624	
Residual......	36	4,143.75	115.10		
Total......	47	17,679.48			

Variance ratio$_1$ is based on the residual mean square.
Variance ratio$_2$ is based on the mean square of the Species x Days interaction.

18 submersion was not significant (t-value of 1.733), but that germination following 34 days submersion was significantly lower than following 18 days (t-value of 9.085).

An unplanned variable in the Nuttall oak tests was that the acorns collected near Plaquemine, Louisiana, were noticeably larger than those collected near Baton Rouge, Louisiana, and Stoneville, Mississippi. Inspection of the data indicated that the large acorns had a higher germination percentage than the smaller ones, and limitation in numbers available had prevented their being equally apportioned among treatments (Table III).

TABLE III. Germination of Nuttall oak acorns by seed source

Seed source	Number of seed lots	Mean germination percentage
Baton Rouge, La..........	4	38
Stoneville, Miss...........	9	39
Plaquemine, La...........	15	45

In order to prevent the partial confounding of treatment with seed source, the data were treated by regression analysis of 6 balanced comparisons: small acorns (Baton Rouge and Stoneville) versus large ones (Plaquemine), Baton Rouge acorns versus Stoneville, swamp water versus tap water, flooded versus controls, 8 & 18 days submersion versus 34 days, and 8 days submersion versus 18. Only the comparison of small acorns versus large ones was significant (variance ratio of 19.538).

Although germination of the small Nuttall oak acorns decreased with length of submersion period, Table IV, the difference did not approach significance.

CONCLUSIONS

Type of water used for submersion did not affect germination of either species.

Germination percentage of cherrybark oak acorns was significantly lowered by 34-day submersion.

Submersion for periods up to 34 days did not significantly affect germination percentage of Nuttall oak acorns.

Large acorns of Nuttall oak had a significantly higher germination percentage than did small acorns.

TABLE IV. Germination of large and small Nuttall oak acorns by flooding duration

Days flooded	MEAN GERMINATION PERCENTAGE	
	Large	Small
8..............	47	42
18..............	44	41
34..............	45	36

The large Nuttall oak acorns showed no indication of being affected by the submersion treatments; small Nuttall acorns appeared to be affected, but were not significantly so; germination of the smallest acorns tested, cherrybark oak, was apparently reduced slightly by 18-day submersion and was highly significantly reduced by 34-day submersion.

The same apparent correlation of size with tolerance of flooding was previously reported for *Nyssa* seed (Briscoe 1957, p. 50). Among seeds of essentially the same structure larger seeds appear to survive flooding better than smaller seeds.

SUMMARY

Acorns of cherrybark and Nuttall oaks were enclosed in open-mesh bags and submerged in swamp water and in tap water for periods up to 34 days; cherrybark acorns were also submerged in sealed bottles of tap water.

Type of water or container did not affect germination of either species.

Cherrybark oak typically grows on sites seldom or never flooded; germination percentage of its acorns was significantly lowered by prolonged submersion.

Nuttall oak is common on sites flooded annually; submersion for periods up to 34 days did not reduce germination percentage of its acorns.

There was some indication that resistance to flooding effects was associated with size of acorn.

REFERENCES

Applequist, M. B. 1959. Longevity of submerged tupelogum and baldcypress seed. LSU Forestry Note **27.** 2 pp.

Bergman, H. F. 1920. The relation of aeration to the growth and activity of roots and its influence on the ecesis of plants in swamps. Annals of Botany **34:** 13-33.

Briscoe, C. B. 1957. Diameter growth and effects of flooding on certain bottomland forest trees. Unpubl. Dissertation. Duke Univ.

———, and A. P. DuBarry, Jr. 1959. A simplified germination test for American sycamore. Tree Planters Notes **35:** 21.

Demaree, D. 1932. Submerging experiments with *Taxodium.* Ecology **13:** 258-262.

Horton, J. S., F. C. Mounts, and J. M. Kraft. 1960. Seed germination and seedling establishment of phreatophyte species. Rocky Mt. Forest & Range Expt. Sta. Paper **48.** 26 pp.

Hosner, J. F. 1957. Effects of water upon the seed germination of bottomland trees. Forest Science **3:** 67-70.

Shunk, I. V. 1939. Oxygen requirements for germination of *Nyssa aquatica.* Science **90:** 565-566.

VEGETATION OF THE DRAINAGE-AERATION CLASSES OF NORTHERN INDIANA SOILS IN 1830[1]

Alton A. Lindsey
Department of Biological Sciences, Purdue University, Lafayette, Indiana

Introduction

The precise location of named individual trees recorded in the original General Land Office surveys makes possible determination of soil type at their sites from the large-scale colored maps of counties in official soil reports. Detailed soil maps and land surveyors' records used together also furnish data for more accurate mapping of pre-settlement vegetation than survey records alone, especially in areas where trees were sparse or absent, as dry prairie, wet prairie and other wetlands.

The recently glaciated Indiana terrain north of the Wabash River, prior to artificial drainage, was half wetland (Table I), defined as Classes D and E in the following classification based on slope, porosity, and position. This is a reduction to 5 of the 10 classes on which the familiar soil catena concept is based. The Roman numerals refer to the soil drainage profiles of Bushnell (1944, 1959).

Table I. Original wetland areas of northern Indiana counties. Drainage Class E comprised permanently ponded land. The total wetland area combines Class E with Class D which was seasonally ponded, in winter and spring mainly. Data were compiled from the tables of acreage of specific soil types in the respective County Soil Reports of the U.S.D.A. and Purdue Agricultural Experiment Station

County	Class E		Total Wetland	
	Per cent of County	Acres	Per cent of County	Acres
Benton......	4.6	12,012	69.2	180,695
Cass........	7.4	19,654	36.9	98,006
Fulton......	17.0	39,930	36.7	86,201
Kosciusko...	21.8	75,480	31.2	108,027
Lake........	31.1	97,927	50.2	158,070
La Porte....	26.0	99,062	38.6	147,069
Miami......	6.8	16,451	26.8	64,835
Newton.....	23.9	63,172	45.3	119,737
Noble.......	16.1	42,452	32.4	85,432
Porter......	29.7	78,883	35.7	94,819
St. Joseph...	20.5	60,877	33.7	100,076
Starke......	54.8	108,022	60.5	119,257
Steuben.....	12.2	23,814	31.8	62,073
White.......	36.2	117,462	56.0	181,718

Class A. Excessively well drained soils. (V-VI)
Class B. Well drained soils. (III-IV)
Class C. Slowly draining soils. (I-II)
Class D. Seasonally ponded soils. (VII-VIII)
Class E. Permanently ponded soils. (IX-X)

The 14 counties surveyed by modern airphoto methods (Table I) comprise 3,224,121 acres of which 1,606,015 acres (or 50%) were classified by the U.S.D.A.—Purdue Agricultural Experiment Station soil survey as the soil types which represent the wetland classes D and E. The shallower wetlands (D) covered 750,817 acres or 23% of these counties, and the deep wetlands (E) made up 855,198 acres or 27%.

Richason (1960) designated as wetlands also the soils which I am calling Class C; he published a map which therefore shows much more than half of Indiana north of the Wabash as wetland originally. Besides the county soil surveys, corroborative evidence for the former prevalence of wetlands has come from the land description forms and the plats of the early land surveys, the disappearance of even large lakes mapped therein (e.g., Beaver Lake and English Lake), historical writings reviewed by Lindsey (1960), and the location of old towns and cemeteries.

Class D soils probably were ponded at least 6 months of the normal year, and Class E soils were ponded or saturated throughout it (Bushnell 1960). The D soils often extended across the bottoms of shallow depressions and branching "incipient drainageways." But in many cases they merely bordered the deeper E depressions and were consequently less well contained. The dark tone of D and E soils on airphotos of Late Wisconsin terrain contrasts with the light tone of the A-C, producing a characteristic mottling.

From the available evidence, it appears that Class D lands supported wet prairies and sedge meadows, seasonally ponded lowland forests, and the shallower (wooded) swamps in the deeper depressions of the D terrain, whereas Class E supported *Spartina* (slough grass), cattail marshes, most swamps, and all bogs. In the wet prairie of class D, the dominant *Andropogon gerardi* grew taller than on the 3 upland drainage classes. Benton County, where the former predominance of bluestem prairie is common local knowledge, was 69% wetland before artificial drainage (Jones and Brill 1917). Finley and Potzger (1952) stated "Only Benton County was predominantly prairie." Barce (1925) described

> . . . mile upon mile of the early prairie, covered in most places with giant blue-stem. . . . A party of land hunters riding through Benton County in the fall of 1824 and following the line of an old Indian trail, found blue-stem so high that a horseman could tie the ends over the top of his head.

In a historical account of Jasper and Newton Counties, Hamilton and Darroch (1916) wrote

> On the high lands the grass did not reach its normal height, while on the lower lands its growth was of astonishing proportions, frequently reaching a height which would hide a man on horseback, and thus would tend to create the illusion of a perfectly level plain. . . . Then the timber, save along the rivers, was marked only by scattered oaks and hickories, which favoring localities preserved from the annual fires which swept the prairies.

Methods

For 7 counties of the central portion of northern Indiana, vegetational attribute tables were prepared (for each county separately and all combined) for each of the 5 drainage-aeration classes of soil. Township grids arranged north-south on long paper rolls were used for

---

[1] The study was supported by the Lands Division, United States Department of Justice.

recording pertinent data at line intersections, as read from microfilm of the surveyors' tree record form. The land surveys (G.L.O. 1828-) had been carried on in 1828-1832.

The 110 named soil types of northern Indiana were grouped into classes A-E. By reference to the colored soil map, each tree record on the township grid roll was marked in one of 5 different colors to indicate the drainage—aeration class at its site. Indeterminable borderline cases were left unmarked. From these completed township grids the data for the attributes tables were obtained, disregarding reproduction-size stems below 4 in. dbh. Since the early surveyors had recorded 4 trees at exterior corners (except at township corners), the quarter method (Cottam *et al.* 1953) was applied in part. On interior and township corners where only 2 trees were noted, density figures were obtained by the closest individual method (Cottam and Curtis 1956). The 2 sets of results were merged by proportional weighting. For mean diameter and absolute and relative basal area, all trees (4 in. dbh and over) having diameter estimates were utilized. The mean dbh for the given species, considered with its density per acre, enables one to visualize the forest somewhat better than does basal area and density. Mean diameters reported are actual means from the raw data, rather than indirect derivations. Basal area per acre was computed for each species by converting its mean dbh to basal area and multiplying this by density per acre. Relative basal area is the percentage (of the combined basal areas of all species as 100) contribution which was made by the particular species.

Large scale wetlands maps were copied on tracing paper from the official county soil maps; all soils of Class D were shown in red, those of Class E in blue, and dry prairie soils in yellow. Because of the general areal importance of wetlands, it seemed necessary to segregate major wetland expanses to indicate extensive vegetation under control of extreme edaphic conditions, in order to produce a vegetation map not unduly generalized. In 10 of the 14 counties of Table I, the wetland (D and E) soils comprise more than one-third of the county, and, in 4 of these, more than one-half.

The township grid strips were unrolled side-by-side on a large floor. For mapping purposes, I used only corners representing the well-drained Class B condition, i.e., the median of the upland site moisture gradient. Any one of the 5 classes could form the basis of a separate vegetation map of an extensive area; the one class selected being the most mesic, supported the best expression of the "climatic climax" vegetation, which someone has termed the edaphic climax of the most favorable sites. The other forested upland soils (Classes A and C) were also mapped as either beech-maple or oak-hickory vegetation, as indicated by the forest of the associated Class B sites. The method thus differs from that of Potzger *et al.* (1956) who utilized all tree data provided and lumped them by township to construct map-diagrams for the entire state. These authors included upland ash species in figuring percentages for the beech maple type, whereas for mapping forest types I used only sugar maple and beech, and any species of oak or hickory for the contrasting type. Corners having species of the two different types equally represented did not contribute to the mapping. On type-definite corners of Class B only, then, I placed either white or black cardboard squares to distinguish beech-maple from oak-hickory, so that the patterns, usually quite definite, emerged. These were mapped on the county maps, and the latter finally combined into one (Fig. 1).

The 7 counties thus treated, and the references to the corresponding government soil maps used, were: Cass County (Smith *et al.* 1955), Elkhart County (Jones and Hesler 1914), Fulton County (Rogers *et al.* 1946), Kosciusko County (Tharp *et al.* 1927), Miami County (Tharp and Kunkel 1927), Noble County (Rogers *et al.* 1955), and St. Joseph County (Ulrich *et al.* 1950). The remaining 19 counties, some of which have never had soil surveys, are not cited here in full because the published maps may be located by county name as readily as by authors. The maps published before 1915 are less accurate than subsequent ones based on airphotos and ground surveys. For several counties, unpublished maps from surveys in progress were kindly loaned by Prof. H. P. Ulrich of the Indiana Soil Survey staff, Purdue Agricultural Experiment Station; he also brought soil type nomenclature from the older surveys into conformity with present usage.

Most common names of Indiana trees used by the deputy surveyors circa 1830 are still used today, and practically all are identifiable. Forty-nine species exceeding 4 in. dbh were recorded in the 25 northern Indiana counties. Since cottonwood and aspen were recognized, "poplar" referred to *Liriodendron.* This is indicated also by its great mean diameter. (Kilburn [1959] interpreted "poplar" as *Populus deltoides* in northern Illinois, where forest patches follow stream valleys.) Discrimination in *Quercus* and *Fraxinus* seems remarkable; for 9 oak species and 5 ash the present common names were used. The only peculiarity regarding ash was that *F. pennsylvanica* was apparently termed "swamp ash" in lowland sites and "green ash" on uplands. Black ash was recognized by all surveyors and its habitat confirms its naming. Blue ash (*F. quadrangulata*) was listed rather frequently compared to its known modern status. Its inner bark turns blue on exposure, hence the routine blazing of witness and bearing trees enabled it to be recognized readily. Surveyors wisely refrained from naming hickories to species. The recognition of less usual trees such as prickly ash (*Xanthoxylum*) and "coffee nut" (*Gymnocladus*) enhances respect for their botanical lore. Unfortunately, swamp white oak (*Quercus bicolor*) was not consistently separated from white oak (*Q. alba*), so that I have arbitrarily considered their "white oak" in Class D and E sites as *Q. bicolor.* As *Acer saccharum* and *A. nigrum* were called "sugar," their "maple" referred to the soft maples *A. saccharinum* and *A. rubrum* without distinction.

Authors of the scientific names used may be found in Little (1953).

Meyer (1952) was unable to interpret the term "barrens." Because of the frequent mention by surveyors of "oak grubs" and "stool grubs" (sprouting thick woody stems lying just below ground), I believe "barrens" were oak-brushlands and scrub, maintained so by fires. This vegetation type was noted frequently along the prairie border.

RESULTS AND DISCUSSION

Vegetation Type Distribution

After completion of the generalized map of pre-settlement vegetation (Fig. 1), it was compared with Wayne's (1958) map of glacial geology. There was fair correspondence between vegetation types as shown and the land features reflecting different modes of glacial origin and history. Wetlands occurred in areas of ground moraine, lake sediments, valley train and outwash plain sediments. Also, the high water table areas of old dune sands in Starke, Pulaski, and northern White counties had extensive wetlands, which supported wet prairie and marsh. These 2 latter types dominated the wetlands of northwestern Indiana in the prairie region, whereas the

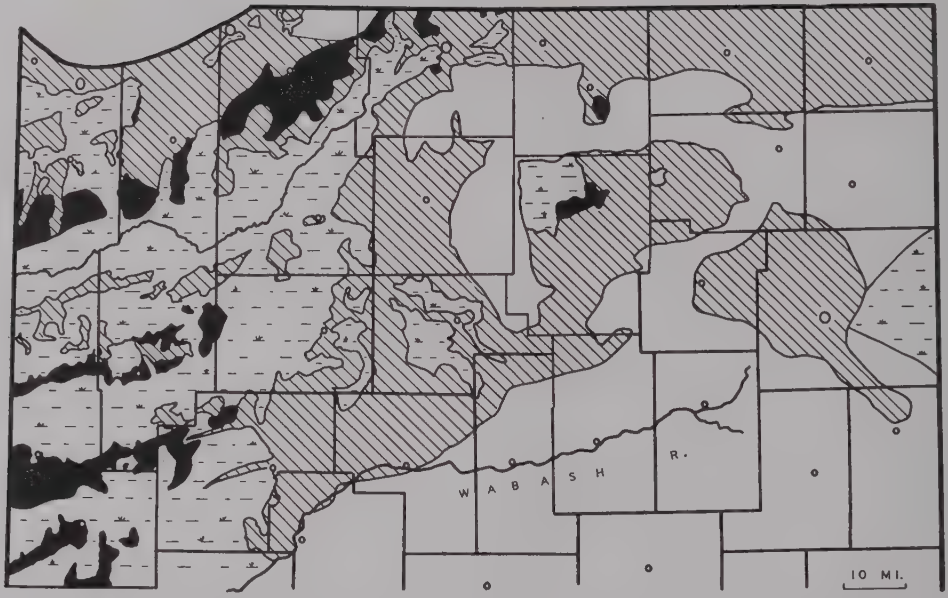

FIG. 1. Vegetation types of the northern third of Indiana in 1830, as determined from original land survey records and modern large-scale soil maps of counties. Black, dry prairie; white, beech-maple forest; hachured, oak-hickory forest; grass-water symbol, wetlands of Classes D and E (see text) supporting wet prairie, marsh, (wooded) swamp, and bog vegetation. Circles indicate cities and towns, chiefly county seats.

timbered region of northeastern Indiana had many swamps and bogs. These wooded wetlands had a large aggregate area, but were relatively small and widely scattered; only the few larger ones are shown in Figure 1. That along the Indiana-Ohio boundary occupied the former bed of glacial Lake Maumee.

Dry prairie in northwest Indiana was typical of the rough topography of end moraines. Dry prairie areas formed several parallel bands showing a general southwest-northeast trend, each continuous or interrupted by wetland depressions. The few prairie patches in northcentral Indiana occurred on valley train and outwash and plain sediments.

Oak-hickory vegetation showed high correlation with better-drained dune sand areas, above the wetland depressions. In the northcentral and northeastern counties, oak-hickory (rather than dry prairie as in the northwest) characterized end moraines, whereas beech-maple tended to occupy ground moraines. Although beech-maple covered many end moraine lands, and oak-hickory considerable areas of ground moraines, the general correlation in the opposite way was clear enough. Of course, some forests were so mixed that the representations of beech-maple and oak-hickory species-groups were about equal.

Considering only Class B substrates, differentiation of beech-maple from oak-hickory in the (most studied) 7 counties forming the central third of Figure 1 cannot be attributed to macroclimatic differences. The present climate shows regular increases of annual precipitation and mean annual temperature from north to south. No known climatic factor or index of combined factors yields a pattern remotely resembling the complex interdigitation of vegetation types. (Personal communication, State Climatologist L. A. Schaal, 1960). These types, however, definitely tend to follow substrates produced by different modes of glacial action, even though I minimized edaphic differences by mapping forest types as they occurred on only well drained, median portions of the terrain mosaic. The counties involved are flat and without marked climatic contrasts within each one (or even among them as a group), yet each of the 7 contained extensive areas of both forest types. This points to edaphic rather than climatic segregation. If both types are considered climaxes in this region, polyclimax interpretation is indicated. The monoclimax theorist would call the oak-hickory type here an edaphic subclimax to the climax beech-maple. The trouble with this is that both are well represented, and interdigitate, on similar well-drained, mesic substrates. Naturally there is some range of drainage-aeration conditions within Class B. The more sloping (Profile IV) sites are doubtless more common in end moraine country than on ground moraines. Also, comparing solely within Class B, end moraines are probably more porous than ground moraines, therefore more deeply and thoroughly leached. The resulting higher acidity on end moraines would favor oak-hickory over beech-maple. Another difficulty arises in the monoclimax viewpoint. In this transition region, the oak-hickory, however interpreted, formed at most a narrow band between prairie and beech-maple. If we reduce oak-hickory in northern Indiana to edaphic subclimax status, this places two types having sharply contrasting mesophily, prairie and beech-maple, in direct contact over a wide front, as theoretical climatic climaxes. To avoid this anomaly, one might argue that there is no real prairie climate in Indiana, that the wet prairie was determined by poor drainage (and fire to some extent), the dry prairie by excessive drainage, and fire to a large extent. But since drainage and fire were also very important farther west where the climate was oftener recognized as favoring tall grass prairie, can a general line be drawn anywhere between prairie as climatically controlled and prairie determined by site and fire within a forest climate? More fundamentally, if the oak-hickory bordering zone occurred under beech-maple climate, the tall grass prairie was so largely within a forest climate, and the western plains vegetation was controlled biotically under a climate favorable to taller grass, would not polyclimax or continuum viewpoints serve better than a monoclimax one needing continual reservations and circumlocutions?

Forest Composition and Structure

The chief results of the study are presented in Tables II-V, which show the attributes of pre-settlement vegetation for site drainage-aeration Classes A, B, and C for higher ground, and Class D for the shallower wet depressions. This use of water relations rather than parent materials, soil chemistry, etc., as a basis of organization cuts directly across the catenas, and is thought to furnish a more realistic view of the forest of 1830 than would any other single basis of grouping the data. The forest has been treated as a unit for this analysis, without distinction of type. Also, spatially separate stands cannot be recognized; the results include numerous open glades and meadows, so long as they show soils developed under forest, averaged together with densely crowded and other stands. (Whenever a tree was recorded, at whatever distance, I included it.) For this reason, the absolute (per acre) figures for density and basal area are low when compared with modern analyses of distinct and continuous stands of undisturbed forest.

TABLE II. Attributes of tree species (from individuals at least 4 in. dbh) circa 1830 on excessively well drained (Class A) soils in 7 mid-northern Indiana counties, namely, Cass, Elkhart, Fulton, Kosciusko, Miami, Noble, and St. Joseph Counties

	Mean Diameter	Density per acre	Relative Density	Basal Area per acre	Relative Basal Area
Quercus alba............	18.8″	4.98	44.1%	9.60	53.6%
Q. velutina..............	18.9	1.59	14.1	3.10	17.3
Carya spp..............	10.2	1.05	9.26	0.590	3.29
Fagus grandifolia.........	15.4	0.73	6.43	0.944	5.27
Quercus macrocarpa.......	14.2	0.46	4.05	0.500	2.79
Q. muehlenbergii.........	14.9	0.41	3.64	0.496	2.77
Acer saccharum..........	16.5	0.33	2.88	0.490	2.74
Quercus rubra............	19.9	0.30	2.68	0.648	3.62
Ostrya virginiana.........	7.8	0.27	2.43	0.090	0.50
Ulmus americana.........	13.2	0.22	1.92	0.208	1.16
Fraxinus spp.............	13.0	0.30	2.68	0.279	0.56
Tilia americana..........	14.6	0.11	1.01	0.127	0.71
Liriodendron tulipifera....	25.4	0.11	0.96	0.386	2.15
Juglans nigra............	18.4	0.10	0.86	0.184	1.03
Other species............	—	0.34	3.04	0.274	1.53

The overall average diameter of stems 4 in. dbh and over was 16.7 in. on Class A sites, 16.3 on Class B, 15.8 on Class C, 16.1 on Class D, and 14.1 on Class E. Number of stems of all species combined was 11.3 on Class A, 32.3 on Class B, 18.4 on Class C, 19.7 on Class D, and 1.9 on Class E. The great diameter on Class A sites is probably significant, as large girth and low spreading crowns would be expected where density averages only 11.3 stems per acre. It is especially typical of *Quercus alba* on dry sites. This species on Class A had an importance percentage (average of relative density and relative basal area) of 48.8; *Q. velutina* had 15.7%, *Carya* spp. 6.27 and *Fagus* 5.85.

TABLE III. Attributes of tree species circa 1830 on well-drained (Class B) soils in the 7 mid-northern Indiana counties named for Table II

	Mean Diameter	Density per acre	Relative Density	Basal Area per acre	Relative Basal Area
Fagus grandifolia.........	15.4″	7.89	24.5%	10.22	20.2%
Quercus alba............	20.7	6.72	20.8	15.71	31.0
Acer saccharum, A. nigrum.	15.7	2.95	9.17	3.98	7.87
Carya spp..............	11.3	2.43	7.53	3.03	5.99
Fraxinus spp.............	12.9	2.36	7.31	2.14	4.23
Ulmus americana.........	15.1	1.65	5.10	2.08	4.11
Quercus velutina..........	19.1	1.46	4.48	2.91	5.74
Ostrya virginiana.........	7.4	1.43	4.43	0.431	0.85
Quercus rubra............	23.2	1.18	3.67	3.46	6.85
Tilia americana..........	15.7	0.82	2.55	1.10	2.18
Liriodendron tulipifera....	24.0	0.76	2.35	2.39	4.72
Quercus macrocarpa.......	19.0	0.45	1.39	0.883	1.75
Juglans nigra............	19.2	0.39	1.21	0.785	1.55
Quercus muehlenbergii.....	14.8	0.16	0.51	0.191	0.38
Other species............	—	1.60	4.95	1.278	2.53

TABLE IV. Attributes of tree species circa 1830 on slowly draining (Class C) soils in the 7 mid-northern Indiana counties named for Table II

	Mean Diameter	Density per acre	Relative Density	Basal Area per acre	Relative Basal Area
Fagus grandifolia.........	14.6″	6.36	34.6%	7.36	28.0%
Quercus alba, Q. bicolor....	21.5	2.56	13.9	6.55	24.9
Acer nigrum, A. saccharum.	16.9	1.50	8.17	2.36	8.9
Carya spp..............	12.9	1.19	6.48	1.07	4.08
Fraxinus (except *F. nigra*).	15.6	1.09	5.92	1.45	5.50
Ostrya virginiana.........	6.5	0.85	4.60	0.196	0.75
Ulmus americana.........	15.2	0.73	3.94	0.920	3.50
Quercus velutina..........	21.0	0.71	3.85	1.71	6.49
Tilia americana..........	16.8	0.62	3.38	0.955	3.63
Quercus rubra............	19.0	0.61	3.29	1.20	4.57
Q. macrocarpa...........	16.8	0.38	2.07	0.585	2.22
Fraxinus nigra...........	12.6	0.36	1.97	0.312	1.19
Liriodendron tulipifera....	21.3	0.21	1.13	0.517	1.97
Juglans nigra............	13.3	0.15	0.84	0.145	0.55
Quercus muehlenbergii.....	13.1	0.12	0.66	0.113	0.43
Other species............	—	0.97	5.26	0.880	3.35

TABLE V. Attributes of tree species circa 1830 on seasonally ponded (Class D) soils in the 7 mid-northern Indiana counties named for Table II

	Mean Diameter	Density per acre	Relative Density	Basal Area per acre	Relative Basal Area
Fagus grandifolia.........	15.2″	4.59	23.3%	5.78	21.9%
Quercus bicolor...........	20.5	2.54	12.9	5.82	22.0
Ulmus americana.........	16.3	2.20	11.2	3.19	12.1
Fraxinus (except *F. nigra*).	11.2	1.75	8.9	1.20	4.5
Acer saccharinum, A. rubrum...........	12.3	1.31	6.7	1.08	4.1
Fraxinus nigra...........	14.9	1.27	6.4	1.54	5.8
Quercus macrocarpa.......	18.7	0.97	4.9	1.85	7.0
Acer nigrum, A. saccharum.	17.4	0.64	3.2	1.06	4.0
Ironwood...............	7.1	0.58	3.0	0.16	0.60
Populus grandidentata, P. tremuloides.........	9.2	0.51	2.6	0.24	0.89
Larix laricina...........	4.0	0.05	0.23	0.004	0.02
Salix spp...............	7.2	0.30	1.5	0.085	0.32
Platanus occidentalis......	20.5	0.25	1.3	0.573	2.17
Ulmus rubra............	15.9	0.19	0.98	0.262	0.99
Other species............	—	2.56	13.0	3.57	13.5

The total basal area per acre irrespective of species was 17.9 sq ft on Class A, 50.6 on Class B, 26.3 on Class C, and 26.4 on Class D.

Since both density and basal area were decidedly greatest on Class B, the latter unquestionably provided the most favorable forest sites on the whole. There the importance of *Quercus alba* was 25.9%, of *Fagus* 22.3, of the hard maples 8.52 and the hickories 6.76%. Thus, the combined importance of white oak and beech was more than threefold that of *Acer saccharum, A. nigrum,* and all *Carya* spp. (There may have been some bias favoring beech, a smooth-barked tree which could have been marked without blazing.)

The forest on Class C (Table IV) was intermediate between those on B and D sites in many respects. In density, beech-maple (43%), not including soft maples, clearly overbalances oak-hickory (31%) species.

The density of trees in the seasonally ponded Class D lowlands was remarkable, exceeding that of all others except Class B. Also, the trees averaged larger than on the other 2 imperfectly drained classes, C and E. The 3 leading species, *Fagus grandifolia, Quercus bicolor,* and *Ulmus americana,* had importance percentages of 45.2, 34.9, and 23.2, respectively.

SUMMARY

By use of modern soil survey maps along with records of early land surveys, the vegetation of the northern third of Indiana was mapped, showing areas of dry prairie, *Quercus-Carya, Fagus-Acer,* and wetlands. Also, the tree species attributes were determined for the 5 different drainage-aeration classes of the soils of 7 mid-northern Indiana counties.

REFERENCES

Barce, Elmore. 1925. Annals of Benton County. Privately publ., Fowler, Indiana.

Bushnell, T. M. 1944. The story of Indiana Soils with descriptions of general soil regions and the key to Indiana soils. Purdue Univ. Agr. Expt. Sta., Lafayette, Indiana.

———. 1959: A story of Hoosier soils. Peda-Products, Lafayette, Indiana.

———. 1960. (personal communication)

Cottam, Grant, J. T. Curtis, and B. W. Hale. 1953. Some sampling characteristics of a population of randomly dispersed individuals. Ecology **34**: 741-757.

——— **and J. T. Curtis.** 1956. The use of distance measures in phytosociological sampling. Ecology **37**: 451-460.

Finley, Dean, and J. E. Potzger. 1952. Characteristics of the original vegetation in some prairie counties of Indiana. Butler Univ. Bot. Ser. **10**: 114-118.

General Land Office Survey Records for Indiana. 1828-1834. Vols. 3, 4, 6, 7, 8. Microfilm made from original volumes in State Archives, Indianapolis.

Hamilton, L. H. and William Darroch. 1916. Jasper and Newton Counties, Indiana. Lewis Publishing Co., Chicago and New York.

Jones, G. B. and R. S. Hesler. 1914. Soil survey of Elkhart County, Indiana. U.S.D.A. and Indiana Department of Geology.

——— **and J. B. Brill.** 1917. Soil survey of Benton County, Indiana. U.S.D.A. Bureau of Soil. Government Printing Office, Washington.

Kilburn, P. D. 1959. The forest-prairie ecotone in Northeastern Illinois. Am Midl. Nat. **62**: 206-217.

Lindsey, A. A. 1960. The landscape and vegetation of Docket 254 Area in 1830. (Unpublished report to U. S. Dept. of Justice.)

Meyer, A. H. 1952. Fundament vegetation of the Calumet Region, Northwest Indiana—Northeast Illinois. Papers Michigan Acad. Sci., Arts, and Letters **36**: 177-182.

Potzger, J. E., Margaret Potzger, and Jack McCormick. 1956. Butler University Botanical Serices **13**: 95-111.

Richason, B. F., Jr. 1960. Wetland transformation in the Wisconsin Drift Area of Indiana. Proc. Indiana Academy of Science for 1959.

Rogers, O. C., A. P. Bell, T. E. Barnes, Sutton Myers, and A. T. Wiancko. 1946. Soil survey of Fulton County, Indiana, U.S.D.A. and Purdue Univ. Agr. Expt. Sta.

———**, P. T. Veale, S. Myers, J. E. Combs, and G. H. Robinson.** 1953. Soil survey of Noble County, Indiana. U.S.D.A. and Purdue Univ. Agr. Expt. Sta.

Smith, L. R., W. J. Leighty, D. R. Kunkel, and A. T. Wiancko, and O. C. Rogers. 1955. Soil survey of Cass County, Indiana. U.S.D.A. and Purdue Univ. Agr. Expt. Sta.

Tharp, W. E., E. D. Fowler, L. S. Troth, and H. R. Beyer. 1927. Soil survey of Kosciusko County, Indiana. U.S.D.A. and Purdue Univ. Agr. Expt. Sta., Government Printing Office, Washington.

——— **and D. R. Kunkel.** 1927. Soil survey of Miami County, Indiana. Part 1., Bur. Chemistry and Soils and Purdue Univ. Agr. Expt. Sta. Washington, D. C.

Ulrich, H. P., A. P. Bell, S. Myers, L. E. Allison, B. A. Krantz and P. T. Veale. 1950. Soil survey of St. Joseph County, Ind. U.S.D.A. and Purdue Univ. Agr. Expt. Sta.

Wayne, W. J. 1958. Glacial Geology of Indiana (Map, 1:1,000,000 scale). Indiana Department of Conservation.

AN ANALYSIS OF MAXIMUM SUMMER TEMPERATURES INSIDE AND OUTSIDE A FOREST

HAROLD C. FRITTS
Laboratory of Tree-Ring Research, University of Arizona, Tucson

One of the major problems in ecological studies is the difficulty of adequately evaluating the multiplicity of micro-environments. Frequently the lack of equipment and time limit the investigator to environmental measurements taken at one location and these data are assumed to be relative to those of other areas under study. Microclimatologists recognize this problem and have long sought to formulate the principles governing the environmental relationships which in turn would allow a reliable estimate of diverse habitats from a limited set of measurements

(Geiger 1957, Wolfe *et al.* 1949). This paper is an attempt to analyze certain relationships in respect to maximum temperatures.

Kucera (1954), Larson (1922), Pearson (1914), Selleck and Schuppert (1957), Sparkes and Buell (1955) and Vaartaja (1954), among others, have shown that during the summer season maximum temperatures in the forest are consistently lower than those in the open. The cause of this is generally attributed to interception of solar radiation and deflection of air currents by the forest canopy. Chapman *et al.* (1931) compared mean daily temperatures in a maple-basswood forest, tamarack forest, and dune blow-out. They obtained significant correlations (*r* values of .90 to .91) and concluded that weather records give a fair index of air temperatures in the immediate climatic area. However, individual temperatures in their study sites, especially those during the day, deviated markedly from Weather Bureau readings. Wolfe *et al.* (1949) found that minimum temperatures recorded by the weather bureau were fair estimates of minimum temperatures at certain stations in a mature forest, but the maximum temperatures exhibited only a poor relationship.

METHODS AND RESULTS

The area studied is a ravine forest 2 miles south southwest of Charleston, Illinois. The ravine drains in an east north-east direction and is 350 ft wide and 50 ft deep where the temperature measurements were obtained. The south-facing slope ranges from 20-40%, while the middle and lower north-facing slope ranges from 45-60%. The south-facing slope and upper north-facing slope (where the slope is less than 40%) are dominated by white oak (*Quercus alba* L.), shagbark and pignut hickory (*Carya ovata* (Mill) K. Koch and *C. tomentosa* Nutt.) with black oak (*Q. velutina* Lam.) becoming more abundant on the upper parts. The middle and lower north-facing slope as well as the lower 15 to 20 ft of the south-facing slope is dominated by sugar maple (*Acer saccharum* Marsh.) associated with red oak (*Q. rubra* L.), shagbark hickory and pignut hickory. At the time of the study, the total basal area per acre for trees over 2½ in. dbh was 137.2 sq ft in the white oak community and 79.6 sq ft in the sugar maple community, with 249 and 176 trees per acre respectively. The understory consisted mainly of sugar maple saplings and was most dense on the lower south-facing slope.

Max-min thermometers (Taylor-Six's type) with aluminum shields were mounted 5 ft above ground, either on the north side of trees or on the north side of instrument shelters, which were strapped to trees. Four stations at different locations in the ravine forest were used in the analysis (Table I). Other thermometers in adjacent sites indicated that these 4 locations provided typical readings for the respective exposures occurring in the ravine. Station 1 was in the white oak community and stations 3 and 4 in the sugar maple community. Station 2 was located in a rather abrupt transition between the 2 forest types. Temperatures in the open were measured with standard Weather Bureau maximum and minimum thermometers housed in a home-made white louvered instrument shelter, located 5½ ft above the ground in the center of a level clearing 155 ft in diameter. The screening angle (Geiger 1957) from the top of the shelter averaged 250.

Daily maximum, minimum, and current temperatures were read in the late afternoon or early evening. When the temperature at time of reading and setting was higher than the maximum on the following day, the recorded maximum was discarded. Complete data were obtained for 32 days from June 5–July 19, 1959. The period was characterized by generally warm, sunny weather with low rainfall of less than 0.10 in. occurring on 4 of the measured days and a drought-breaking rain of 1.36 in. occurring on July 18. Soil temperatures at the 4 in. depth ranged between 60 and 70°F and were essentially the same in all sites, while soil moisture dropped to wilting per cent toward the end of the period.

TABLE I. Site, per cent slope and elevation above stream of each forest thermometer station

Station	Site	Per cent slope	Elevation in feet above stream
1.......	Upper south-facing	25	40
2.......	Lower south-facing	35	18
3.......	Ravine bottom	5	7
4.......	Mid north-facing	60	29

Regression equations were computed for maximum temperatures at each station (Y_1, Y_2, Y_3, and Y_4) in relation to the maximum temperature recorded in the clearing (Table II). All regression and correlation coefficients are significant from zero ($P. < .01$). The coefficients of determination (r^2) indicate per cent variance accounted for in each regression (Ezekial and Fox 1959). It is apparent that a high per cent of variance (71-86%) can be accounted for by a simple linear relationship. The poorest fit was between temperatures in the open and those in site 3 at the bottom of the ravine, where the temperature values varied the least.

TABLE II. Coefficients of determination (r^2), standard errors, means, and standard deviations for simple linear correlations and regressions of maximum temperatures at various forest sites with maximum temperatures occurring in a nearby clearing; $n = 32$

Site	Coefficient of determination	Standard error of estimate	Mean	Standard deviation
Y_1............	.850	1.72	87.5	4.61
Y_2............	.861	1.67	83.7	4.67
Y_3............	.714	2.12	82.3	4.03
Y_4............	.809	1.84	83.0	4.29
Clearing temperature...			90.1	4.61

Differences in mean maximum temperatures between the several stations were tested for significance. Station 1, on the upper south-facing slope, as well as the station in the open, were significantly different from those in all other sites ($t > 3.62$, $P. < .001$). No other combination differed significantly.

Comparison of the mean squares (covariance analysis, Snedecor 1956) indicates that 1) all samples are drawn from populations with a common variance, 2) no significant differences occur between the sample regression coefficients, but 3) the constant for regression Y_1 on x is significantly higher than all others ($P. < .001$), while Y_2 on x differs significantly from Y_3 on x at the .01 level. Values for maximum forest temperatures were estimated from the regression equations (Table III).

A multiple regression analysis (Ezekiel and Fox 1959) was used to evaluate the relative influence of 4 factors on the temperatures in the forest. Differences in daily maximum temperatures (Y_1) between the open field and each forest station were computed and analyzed in terms

TABLE III. Estimated maximum temperatures of forest sites based on selected maximum temperatures in the clearing as determined from regression equations

	Degrees F		
Max. temp. in clearing	*80*	*90*	*100*
Site 1	78.2	87.4	96.6
Site 2	74.2	83.6	93.0
Site 3	74.9	82.2	89.6
Site 4	74.6	82.9	91.3

TABLE IV. Standardized partial regression coefficients, correlations, and other values obtained in multiple regressions of differences between maximum temperatures of the clearing and each forest site; n = 32

Standardized partial regression coefficients	Y_1	Y_2	Y_3	Y_4
b_1 Average wind	− .589*	− .650*	+ .214	− .014
b_2 Clearing temp.	+ 1.012***	+ 1.102***	+ 1.068*	+ 1.291***
b_3 Solar radiation	− 7.034***	− 3.256**	− 1.985	− 1.522
b_4 V.p.d. x soil moist.	+ 7.160***	+ 9.993***	+ 4.129*	+ 8.502***
Adjusted *r*	.830***	.784***	.621**	.801***
Per cent variance accounted for	69.000	61.500	38.700	64.200
Adjusted standard error of estimate	1.003	1.083	1.906	1.190
Mean Y	2.590	6.380	7.780	7.090
Standard deviation Y	1.829	1.773	2.472	2.022

* Significant at .05 level.
** Significant at .01 level.
*** Significant at .001 level.

of wind velocity (x_1), maximum temperature in the clearing (x_2), solar radiation (x_3), and the product of vapor pressure deficit and average available soil moisture at 4 in. (x_4). The wind data are average mph for hourly readings made between 8:00 and 19:00 cst, 30 ft above ground, 7 miles west of the study area. Solar radiation values are the daily total of hourly readings in gram calories/min./cm^2 as measured by a pyrheliograph 2 miles north of the study area. Vapor pressure deficit values are daily, bi-hourly totals (7:00-19:00 cst) calculated from hygro-thermograph recordings made in the shelter outside the forest. Soil moisture was ascertained daily from 18 fiberglas Colman units located on the several sites throughout the forest.

Average wind was included because it was thought to be inversely related to these temperature differences due to increased circulation with higher wind velocities; temperature in the clearing, because it was thought to be positively correlated (Table III); and solar radiation, because it was thought to be negatively correlated due to greater light penetration through the canopy with high radiation intensities. When preliminary analyses using these 3 variables failed to account for a large part of the variation in Y, it was noted that the data appeared inversely related to the intensity of the approaching drought. Since Thornthwaite and Hare (1955) demonstrated that a decrease in cooling power of evapo-transpiration is associated with a decrease in available soil moisture, an estimate of this variable was thought necessary if a significant correlation was to be obtained. A combination of vapor pressure deficit and available soil moisture was felt most appropriate. Since the effect of one is dependent upon the presence of the other and both are positive and linear within the range of soil moisture occurring during the study period (Kuiper and Bierhuizen 1958), the product of the 2 was used as a fourth independent variable. Wind was also thought to be an important factor affecting evaporation (Kucera 1954) and its product with the other 2 factors was also tried, but the results obtained exhibited a much poorer correlation.

The partial regression and correlation coefficients for predicting temperature difference by means of the above 4 variables were tested for significance and partial coefficients transformed to standardized values (Table IV) (Snedecor 1956) so that the relative contribution of each variable to the temperature difference could be ascertained.

It is evident from Table IV that wind was a significant factor in reducing the temperature difference on only the south-facing slope (Y_1 and Y_2) and is less effective than any of the other 3 variables. High maximum temperatures in the clearing corresponded with large temperature differences in all sites, especially at the bottom of the ravine where temperatures varied least (Table II). Increased solar radiation reduced the temperature difference in proportion to exposure of site. Thus site 1 shows the largest coefficient; sites 2 and 3, intermediate in exposure, have a coefficient ½ that of site 1; and site 4, on the north-facing slope, shows the poorest relation. Vapor pressure deficit times soil moisture was of major significance on all sites, indicating a marked cooling effect of evapo-transpiration.

DISCUSSION AND CONCLUSIONS

It is apparent from these data that daily variations of maximum temperature in the forest are closely related to the variations occurring in the clearing, even though the average values may be significantly different. The mean maximum temperature on the upper south-facing slope (oak-hickory site) is closer to the mean maximum temperature in the clearing than to that occurring at any of the other 3 locations (sugar maple sites). However, when temperatures in the clearing range near 90-100°F, the lowest maximum temperatures in the forest are at the bottom of the ravine, and the next lowest are on the north-facing slope. But when maximum temperatures are near 80°F in the clearing, sites 2 and 4 on the less exposed slopes have maximum temperatures which are on the average as low or lower than those occurring near the ravine bottom. Relatively low variation in maximum temperatures in the ravine bottom is presumably due to the low amount of incoming radiation and to the ameliorating influence of the nearby opposing slopes.

Differences occurring between maximum temperatures inside and outside the forest can be attributed to differences in the energy balance of the respective sites. On the upper south-facing slope where the canopy is more open, a larger quantity of solar radiation not only reaches and enters the canopy but is ultimately absorbed by the lower sapling and herbaceous layers where it may heat the air. If there is sufficient soil moisture and the vapor pressure deficit is high, a part of this energy will be dissipated through evapo-transpiration. With a reduction in incoming radiation during cloudy weather, the continued absorption of heat by evaporation at the forest floor causes a decline in temperature of the surrounding air. Wind, although apparently less important, may also effect the temperature difference by increasing circulation which both decreases air temperatures outside and increases temperatures inside the forest.

On the lower south-facing slope where the proportion of radiation reaching the lower forest levels is less, variations due to changes in evapo-transpiration are emphasized. At the ravine bottom and on the north-facing slope such a small proportion of direct radiation reaches the forest floor that the coefficient for this variable drops below the level of significance leaving evapo-transpiration as the most effective variable considered in this analysis. In all 4 sites, the general ameliorating influence of the forest canopy and opposing slopes causes a temperature reduction which is greatest when outside temperatures are highest.

The relationships suggested above are substantiated by the actual temperature data (Fig. 1). A greater difference between forest and clearing temperatures can be noted when the clearing temperatures are high (days 4, 8, and 16) than when they are low (days 6, 18, and 26). However, on cloudy days the maximum temperatures on the south-facing slope drop markedly lower than those in the clearing (days 5, 20, and 21). When v.p.d. times soil moisture is high (1st 10 days), the cooling effect of evapo-transpiration maintains low forest temperatures, especially on the north-facing slope where incoming radiation is lowest. On the 6th day, when evapo-transpiration was probably at its maximum for the period, temperatures on the north slope deviated markedly. Later in the season, as the evapo-transpiration potential became less with the approaching drought, forest temperatures on both the north- and south-facing slopes became more like those in the clearing until the trend was somewhat reversed on the 31st day by the rain, which broke the drought.

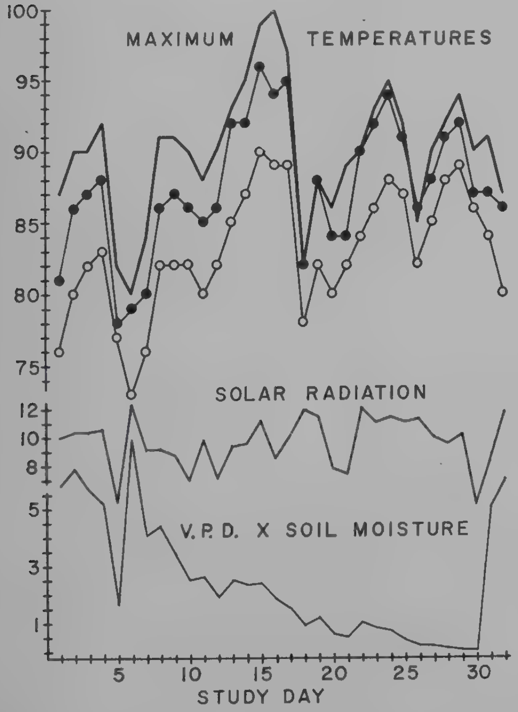

Fig. 1. Maximum temperatures in the clearing (solid line), on the south-facing slope (solid dots), and on the north-facing slope (open dots) plotted with solar radiation (total gram calories per cm^2/60), and the product of vapor pressure deficit and volume soil moisture at the 4 in. depth. The study day number represents the sequence of daily observation, but due to occasional missing data, does not represent a continuous sequence of days.

The actual amount of temperature change associated with each variable can be calculated by substituting the range of that variable in the multiple regression equation. The observed variation in wind (1-22 mph) is associated with a temperature difference on the south slope of 1.5°F, while the variation in solar radiation (5.2-12.2) caused a temperature difference amounting to 5.0°. However, the range in product of v.p.d. and soil moisture (0-7.4) is associated with a temperature difference of 5.3° on the north-facing slope, and the range in clearing temperature (80-100°F) is associated with a 6.1° change in temperature difference at the bottom of the ravine.

The fact that these maximum temperature differences occur may be of major importance to the local distribution of tree species. On the gray-brown podzolic soils of central Illinois, white and black oaks grow in abundance in the warmer and more variable temperature regime of the south-facing slopes and uplands, while in the cooler ravines and north-facing slopes the more mesic red oak and sugar maple reach their best development. These species appear to extend onto the upland only in the denser undisturbed oak-hickory forests or where the soils are of prairie origin (Calef 1953). A difference in the growth-temperature response of a white oak and a sugar maple growing on the lower south-facing slope has already been suggested (Fritts 1959). This emphasis on maximum temperature as a causal factor does not exclude soil moisture, as undoubtedly differences in frequency of drought are at least equally important in the segregation of these two community types.

The high correlations obtained in this study between maximum temperatures inside and outside the forest indicate that measurements of maximum temperatures in the open may be considered relative to those occurring in the forest. Where estimations of the actual forest temperatures from those in the open are to be obtained, especially for sites in ravines and on north-facing slopes, variations in temperatures should be sampled and regressions calculated. When a very precise estimate of maximum forest temperatures is needed, the relative influence of vapor pressure deficit, soil moisture, solar radiation and wind on the relative temperature relationships should also be considered.

The author is indebted to the American Philosophical Society (Johnson Fund) for their grant, which made this study possible; to Kenneth E. Damann and Francis H. Craig for use of the study area; and to Charley M. White, Phillip D. Sanders, and Robert E. Witters for their able assistance.

References

Calef, R. T. 1953. Flora and ecological analysis of the vegetation of the Funk Forest National Area, McLean County, Illinois. Ill. Acad. Sci. Trans. **46**: 41-55.

Chapman, R. N., R. E. Wall, L. Garbough, and C. T. Schmidt. 1931. A comparison of temperatures in widely different environments of the same climatic area. Ecology **12**: 305-322.

Ezekiel, M. and K. A. Fox. 1959. Methods of correlation and regression analysis, 3rd Edition. John Wiley, N. Y. 548 pp.

Fritts, H. C. 1959. The relation of radial growth to maximum and minimum temperatures in three tree species. Ecology **40**: 261-265.

Geiger, R. 1957. The climate near the ground, 2nd Edition. Harvard Univ. Press. 494 pp.

Kucera, C. L. 1954. Some relationships of evaporation rate to vapor pressure deficit and low wind velocity. Ecology **35**: 71-75.

Kuiper, P. J. C. and J. F. Bierhuizen. 1958. The effect of some environmental factors on the transpiration of plants under controlled conditions. Mededelingen van de Landbouwhogeschool te Wageningen, Nederland **58**: 1-16.

Larsen, J. A. 1922. Effect of removal of the virgin white pine stand and upon the physical factors of site. Ecology **3**: 302-305.

Pearson, G. A. 1914 A meterological study of parks and timbered areas in the western yellow pine forests of Arizona and New Mexico. Mo. Weath. Rev. **41**: 1615-1629.

Selleck, G. W. and K. Schuppert. 1957. Some aspects of microclimate in a pine forest and in an adjacent prairie. Ecology **38**: 650-653.

Snedecor, G. W. 1956. Statistical methods applied to experiments in agriculture and biology, 5th Edition. Iowa St. Coll. Press, Ames. 534 pp.

Sparkes, C. H. and M. F. Buell. 1955. Microclimatological features of an old field and an oak-hickory forest in New Jersey. Ecology **36**: 363-364.

Thornthwaite, C. W. and F. K. Hare. 1955. Climatic classification in forestry. Unasylva **9**: 51-59.

Vaartaja, Olli. 1954. Temperature and evaporation at and near ground level on certain forest sites. Canad. Jour. of Bot. **32**: 760-783.

Wolfe, J. N., R. T. Wareham, and H. T. Schofield. 1949. Microclimates and macroclimate of Neotoma, a small valley in central Ohio. Ohio Biol. Surv. Bull. 41. 267 pp.

PRELIMINARY OBSERVATIONS ON RADIOSENSITIVITY OF ALGAE AND FUNGI FROM SOILS OF THE NEVADA TEST SITE[1]

Lora Mangum Shields,[2] L. W. Durrell,[2] and Arnold H. Sparrow[3]

To evaluate relative radiosensitivity of soil algae and fungi from the Nevada Test Site, 89 soil samples were exposed to different levels of gamma radiation from a Co^{60} source at Brookhaven National Laboratory. Total dosages ranged from 2.5 to 2,560 kiloroentgens (kr)[4] administered at dose rates varying from 190 kr to 245 kr/hr. The maximum exposure was 320 kr for the first series, 1,280 kr for the second and 2,560 kr for the third (Table I, II).

Methods

The soils were taken from the surface and the 3-6 in. depth within one mile of four ground zeros (October series) and in undisturbed control areas (December and March series). Samples were collected in quadruplicate—3 for exposure to different levels of radiation and one for culture as an unirradiated control. Each was sealed in a plastic freezer bag at the collection site. Soil was irradiated in the sealed containers, which were not opened until the time of culturing.

Approximately one-half gram of each specimen was cultured for algae on a sterile sand medium moistened with modified Bristol-Roach solution. Cultures were maintained at room temperature for 6 weeks. To isolate fungi, a sample was transferred aseptically to a Petri dish and covered with warm (45°C) Rose-Bengal agar containing streptomycin to inhibit bacterial growth. Plates were examined at intervals for one to several weeks until no new species were appearing. Cultures were checked for the presence or absence of a species with no attempt to quantitate the relative number of survivors.

Observations

In both controls and treated samples, no difference in radiation injury could be observed between those from ground zeros of two years previously and those from undisturbed vegetation zones. Certain soil algae appear less susceptible to radiation injury than common fungi of arid soils since 3 algal species survived acute gamma exposures of 1,280 kr (Table I). The upper range of tolerance for fungi in the same samples was 640 kr (Table II). *Microcoleus vaginatus,* the algal species consistently showing the highest radioresistance, is the most abundant and widely distributed alga in semi-desert soils.

Eleven taxa of fungi were isolated in culture from the unexposed control series in October, 1959. On the irradiated samples of this first series exposed to from 2.5-320 kr, many plates were seeded with 200 colonies, and the average number was 50-60. *Stemphylium ilicis, Fusarium* sp. and the black *Phoma* were present in all cultures. In the second series, the inventory following 2.5-30 kr total doses included the same species as the control group from these sites. Seeding on the culture plates decreased progressively, however, following 10 or 20 kr and higher exposures. This result agrees with the observation by Stotzky and Mortensen (1959) that growth of a fungal population is increasingly inhibited by gamma doses of 8 to 250 kr. The higher soil moisture level in the December series is reflected in the isolation of a greater number of fungal taxa and the relatively low radioresistance of all species. In the 3rd series, 5 species grew in culture following soil dosages of 640 kr.

The occasional appearance in cultures of irradiated soil of algal and fungal species not found in the control may be explained by sampling error. The lapse of several weeks between the preliminary culturing of controls and of the irradiated samples may sometimes account for the absence of a species following irradiation. A more precise determination of the relation of soil moisture content to radiosensitivity of both algae and fungi is in progress.

---

[1] This is one of a series of studies supported by grants from the Atomic Energy Commission and National Science Foundation.

[2] New Mexico Highlands University, Las Vegas.

[3] Brookhaven National Laboratory, Long Island, New York.

[4] The purpose of this latitude in exposure was to determine parameters of radiation tolerance in these soil microorganisms, an unexplored area.

TABLE I. Algal species developing in culture from 89 samples of Nevada soil following exposure to acute gamma radiation dosages at Brookhaven National Laboratory

Species	*Series 1** No. of cultures in Series (total of 27) in which species grew		HIGHEST LEVEL OF RADIATION SURVIVED		
			*Series 1** Total dose 2.5—320 kr, dose rate 200,000 R/hr	*Series 2** Total dose 2.5—1,280 kr, dose rate 245,000 R/hr	*Series 3** Total dose 80—2,450 kr, dose rate 190,000 R/hr
	before exposure	after exposure			
Microcoleus vaginatus	18	17	320	1280	1280
Nostoc commune	6	1	160	—	—
Chlorococcum humicola	3	4	80	160	—
Phormidium spp.	6	1	80	640	1280**
Synechococcus cedrorum	—	—	—	1280	—
Anabaena variabilis	—	—	—	—	160

* Series 1, collected October 8-12, 1959; irradiated November 17, cultured November 27; Series 2, collected December 19-24, 1959; irradiated March 8, cultured March 21; Series 3, collected March 11; irradiated April 25, cultured May 10.
** *Phormidium tenue.*

TABLE II. Fungi developing in culture from 89 samples of Nevada soil following exposure to acute gamma radiation at Brookhaven National Laboratory

Species**	No. of cultures in Series* (total of 27) in which species grew		HIGHEST LEVEL OF RADIATION SURVIVED		
			*Series 1** Total dose 2.5—320 kr, dose rate 200,000 R/hr	*Series 2** Total dose 2.5—1,280 kr, dose rate 245,000 R/hr	*Series 3** Total dose 80—2,450 kr, dose rate 190,000 R/hr
	before exposure	after exposure			
Stemphylium ilicis Tengwall	22	25	320	80	640
Fusarium sp.	19	22	320	80	640
Phoma sp.	11	11	160	160	640
Penicillium oxalicum Thom	16	3	10	20	—
Pythium sp.	0	1	10	—	—
Coccosporium sp.	0	1	5	—	—
Alternaria tenuis Nees	4	2	—	20	640
Aspergillus fumigatus Fresenuis	6	0	0	20	—
A. wentii Wehmer	—	—	—	20	—
Rhizopus nigricans Ehrenberg	2	0	0	40	160
Mucor sp.	—	—	—	40	—
Streptomyces sp.	—	—	—	—	—
Undetermined fungi	—	—	—	320	—

* Series 1, collected October 8-13, 1959; irradiated November 17, cultured November 25; Series 2, collected December 19-24, 1959; irradiated March 8, cultured March 21; Series 3, collected March 11, irradiated April 25, cultured May 10.
** Four additional taxa in the control series did not appear in any of the irradiated samples: *Stachybotrys atra* (in five control plates), *Aspergillus ochraceus* (in two). *Chaetomium* sp. (in one) and *Cunninghamella* sp. (in one).

SUMMARY

Three algal species in soils of the Nevada Test Site (*Microcoleus vaginatus, Phormidium tenue*[5] and *Synechococcus cedrorum*) survived a maximum of 1,280 kr. total acute gamma radiation in laboratory exposures at Brookhaven. Five taxa of fungi developed in culture following total dosages of 640 kr (*Stemphylium ilicis, Fusarium* sp., *Phoma sp., Alternaria tenuis* and *Streptomyces* sp.).

LITERATURE CITED

Stotzky, G. and J. L. Mortensen. 1959. Effect of gamma radiation on growth and metabolism of microorganisms in an organic soil. *Soil Sci. Soc. of America Proceedings* 23: 125-127.

---

[5] Certain systematists consider *Phormidium* spp. in cultures of desert soils to represent *Microcoleus* spp. which, in the presence of moisture, have grown beyond the enclosing sheath.

A PRAIRIE TO FOREST SUCCESSION IN WOOD BUFFALO PARK, ALBERTA

W. W. JEFFREY[1]

INTRODUCTION

In 1958 and 1959 I undertook ecological studies in the lower Peace River area of Wood Buffalo Park in northeast Alberta. An area at Peace Point shown by Raup (1935) to be prairie had at that time been colonized by shrub and tree species. The fact that Raup (1935) gave an accurate map and comprehensive vegetative descriptions of the prairie and adjoining woods furnished an unusual opportunity for exact documentation of the rate and direction of prairie-forest succession. The observations upon which this note is based were made in early June, 1959.

GENERAL DESCRIPTION OF AREA

Peace Point lies on the north shore of Peace River at 59° 7′N, 112°27′W (Fig. 1), and a ranger station has been there for many years. The river bank is high and steep. No cap of fluvial soil exists on the study area, showing that flooding has not occurred in recent times.

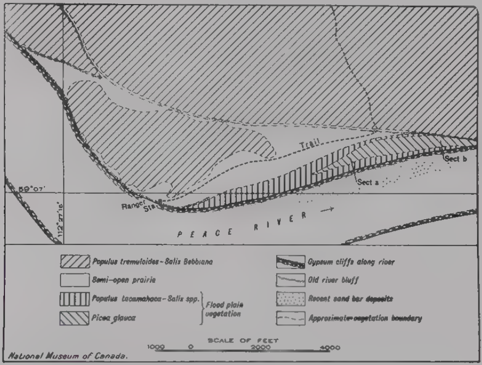

FIG. 1. Map of the Peace Point area (Raup 1935:50).

The soil of the prairie and adjacent forest consists of glacio-lacustrine sediments, of silty—very fine sand and silty—fine sand texture, overlying sporadic till on Devonian gypsum. Beneath both prairie and forest the soil is heavily enriched by organic matter, probably from the decomposition of a present or pre-existent grass sod.

From the river bank the ground runs back several hundred yards in level topography to a bluff (Fig. 1) which Raup (1935) designates "the second bluff." From the top of this bluff similarly level topography stretches north.

At this time, the few remaining prairie openings occur on the lower plain close to the river margin. The remainder of the area is occupied by trembling aspen (*Populus tremuloides* Michx.) forest in which very infrequent solitary white spruce (*Picea glauca* (Moench) Voss) are found. This aspen forest appears floristically distinct from other aspen stands in the region and runs north from the second bluff for several miles.

Status of Prairie—1928

Raup's (1935:45) investigations were carried out in the Peace Point area in 1928. He noted two distinct types of prairie, observing that they "appear to be caused by greater or less desiccation of the soils. The more xerophytic of these, of which *Stipa comata, Avena Hookeri* and *Koeleria cristata* are characteristic or dominant species, is limited to the wind-swept, well-drained margin of the bluff that is just above the present river and to the dry top of the second bluff." (Ibid: 50-51).

The more mesophytic type was "dominated by *Agropyron trachycaulum* var. *unilaterale* and by an assemblage of perennial herbs of which *Geum triflorum, Stachys scopulorum, Geum macrophyllum* var. *perincisum*, and *Galium boreale* are (were) the most prominent." Other characteristic species included *Rosa acicularis* and *Symphoricarpos occidentalis* which were part of an invading group of shrubs from the neighboring aspens woods (Ibid: 51-52).

A map (Ibid: 50) showing the areal extent of the prairie at that date is reproduced as Figure 1. A photograph (Ibid: 42) gives a general view of the prairie then.

Status of Prairie—1959

Since Raup's examination in 1928, the prairie had undergone a noticeable invasion by trembling aspen (Fig. 2). The only mesophytic prairie openings remaining were those near the old wagon trail marked on Raup's map (Fig. 1), along with a small remnant at the foot of the inland bluff. Over ¾ of the area shown as grassland in Figure 1 had undergone transition to closed aspen forest, or was in the process of conversion through an intermediate *Populus tremuloides-Salix Bebbiana* open forest stage.

The present prairie openings subdivided easily into 3 categories: (1) the dry, exposed bluff top community (Ibid: 50-51), which still existed, its component species unchanged; (2) the mesophytic prairie; and (3) a variant of the mesophytic prairie confined to locally well-drained small ridges of the prairie relicts. This type was characterized by the absence of shrubs other than *Artemisia comata* and by *Koeleria cristata* and *Oxytropis splendens.*

Mesophytic Prairie.—Detailed attention was given only to the mesophytic prairie community, since the others mentioned occupied only small areas and were of relatively minor importance. The mesophytic prairie in 1959 was characterized by an abundance of shrubs, typically covering 50-75% of the surface area. The major shrub species were *Rosa acicularis, Symphoricarpos occidentalis,* and *Ribes oxyacanthoides.* Also occurring were *Amelanchier florida, Lonicera glaucescens, Shepherdia canadensis,* and *Salix Bebbiana.*

In the herb layer dominant plants included *Agropyron* spp., *Geum* spp., *Galium boreale,* and *Oxytropis splendens.* Other commonly occurring species were *Viola adunca, Hierochloe odorata, Pulsatilla ludoviciana, Antennaria campestris, Comandra richardsiana, Achillea millefolium, Thalictrum venulosum, Smilacina stellata, Aster* spp., *Vicia americana, Sisyrinchium angustifolium, Cirsium drummondii, Androsace septentrionalis,* and *Fragaria glauca.*

Closed Aspen Forest

The stands of the aspen forest were of variable age, though typically fairly regular in structure as maturity was reached. Near the ranger station they were dense, up to 40 ft high, and composed of stems 2-10 in. dbh. In the closed aspen forest, variations in minor vegetation

---

[1] Forest Research Division, Canada. Department of Forestry, Calgary, Alta.

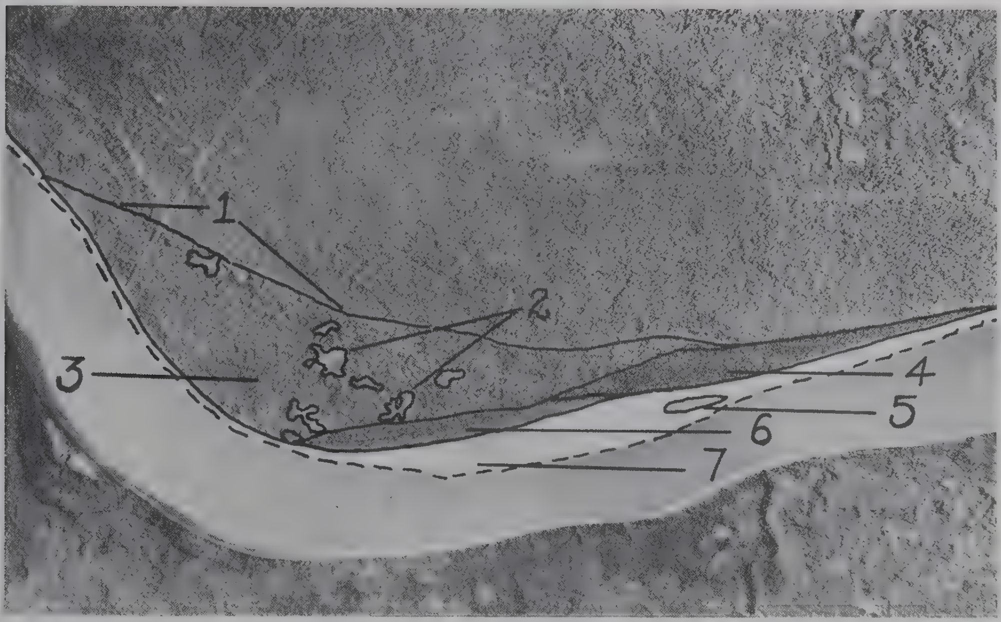

FIG. 2. Aerial photograph A 15163-50 of Peace Point area (taken in September, 1955), showing (1) Second bluff, (2) Prairie remnants, (3) Aspen forest, (4) White spruce forest, (5) Riparian *Salix* spp., established during interval between examinations (1928-59), (6) Balsam poplar forest, and (7) Recent sandbar deposition.

probably reflect the different developmental stages of the forest stands. Species of the prairie tended to persist in the young forest but were much less strongly represented in the older stands. At all stages of development the shrub layer was the most notable, usual dominant species being *Salix Bebbiana* and *Symphoricarpos occidentalis.* Other shrubs included *Amelanchier florida, Rosa acicularis Rubus idaeus,* and *Lonicera glaucescens.* In some older more open stands the *Salix* and *Amelanchier* component assumed in part an underwood position, intermediate between the forest canopy and the shrub layer. Herbs of the closed forest included *Epilobium angustifolium, Lathyrus ochroleucus, Solidago* spp., *Delphinium glaucum, Vicia americana, Aster ciliolatus, Elymus innovatus, Thalictrum venulosum, Fragaria glauca, Smilacina stellata, Pyrola asarifolia, Galium boreale,* and *Achillea millefolium.* Where gaps occurred in the canopy of the closed forest, the openings tended to be shrub-choked, with some herbaceous species of the prairie vegetation beneath the shrubs.

Under the young stands of closed forest structure, the vegetative composition was similar to the above. Many of these stands appeared to have originated through a process of group coalescence whereby previously isolated nests of trees merged to form a continuous forest. More favorable light conditions in zones of coalescence appeared to encourage survival of relict plants of the prairie vegetation for some time after canopy closure.

Aspen—Willow Open Forest

In this forest the "standards" were trembling aspen, and the understory which occupied a position similar to that of coppice in "coppice-with-standards" structure was composed of *Salix Bebbiana, Amelanchier florida* and *Populus tremuloides.* The shrub layer also contained these species, along with *Rosa acicularis* and *Symphoricarpos occidentalis.*

In the herb layer *Elymus innovatus, Arctostaphylos Uva-Ursi, Pulsatilla ludoviciana,* and *Fragaria glauca* were most abundant, with *Thalictrum venulosum, Carex obtusata, Pyrola asarifolia,* and *Achillea millefolium* as concomitant species.

The open forest stage may be a precursor of the closed forest which may thus evolve through stand closure as well as through the coalescence of separate stands previously mentioned.

DISCUSSION

Comparison of prairie status of 1928 and 1959 and of Figures 1 and 2 shows the changes which have taken place during 31 years prior to reassessment. In 1928 a substantial prairie remained; in 1959 it had almost disappeared. Furthermore, such small prairie openings as persisted tended to be dominated by shrubs and to be in the process of colonization by trembling aspen root sprouts around their margins. Moss (1955: 517) mentioned the ability of trembling aspen to invade prairie in this manner.

At Peace Point the drier stations appeared less susceptible to shrub invasion, notably the inland bluff (Figs. 1, 2) whose face remained uncolonized by woody species, though the aspen forest extended from above to within a few feet of the bluff top, and from below to the lower slope of the bluff face. This may indicate that soil drainage and moisture are limiting factors in shrub and tree colonization of grassland vegetation.

Raup's statement (1934: 12-13) that Peace Point derived its name from a meeting of the Cree, Beaver and Slave Indians at some time prior to Alexander Mackenzie's Pacific journey of 1792, leads to the belief that the prairie has long existed and may once have been much larger than in modern times.

Soils of the aspen forest north of the present prairie showed notable similarities to the soils of the present prairie. In fact, the present limits of the *Populus tremuloides—Salix Bebbiana—Symphoricarpos occidentalis* forest, growing on soils of silty sand texture and showing appreciable organic enrichment, may be the original boundaries of the Peace Point prairie. At the same time, the Indian Council mentioned (Raup 1934) may indicate not only that the prairie was sufficiently large to be noteworthy but that it was also a locale well known to the Indians. Lutz (1959) has documented the use of fire by northern aboriginal man and his carelessness towards forest burning. This suggests that the prairie might have been anthropogenic, possibly pyrric, in origin rather than the natural expression of physical environment.

If the present boundaries of this forest type represent the limits of greatest prairie extension, trembling aspen invasion of the prairie must have been effective over a considerable period, since many of the aspen are presently mature. The possible reasons for invasion of the prairie are problematical (Moss 1955, Brink and Farstad 1949) and include, among others, climatic change and recent fire suppression. Similarly, the effect of present bison grazing, grooming and wallowing (Fuller 1960:6) upon the maintenance of remaining prairie openings cannot easily be assessed. Present trends indicate, however, that within a relatively short time the Peace Point mesophytic prairie will effectively have disappeared.

ACKNOWLEDGMENT

Thanks are due to J. S. Rowe for guidance in this work; to H. M. Baldwin, National Museum of Canada, for identification of plant specimens; and to the Laboratory of Forest Biology, Calgary, for photographic assistance.

REFERENCES

Brink, B. C. and Farstad, L. 1949. Forest advance in north and central British Columbia. Canadian Field Nat. **63**: 37.

Fuller, W. A. 1960. Behavior and social organization of the wild bison of Wood Buffalo National Park, Canada. Arctic. **13**(1): 3-19.

Lutz, H. J. 1959. Aboriginal man and white man as historical causes of fire in the boreal forest, with particular reference to Alaska. Yale Univ., School of Forestry, Bull. **65**.

Moss, E. H. 1955. The vegetation of Alberta. Bot. Rev. **21**: 494-562.

Raup, H. M. 1934. Phytogeographical studies in the Peace and Upper Liard River regions, Canada. Contrib. Arnold Arbor. of Harvard Univ. **6**: 1-230.

Raup, H. M. 1935. Botanical investigations in Wood Buffalo Park. National Museum of Canada, Bull. **74**.

RELATIVE IRON REQUIREMENT OF SOME COASTAL AND OFFSHORE PLANKTON ALGAE

JOHN H. RYTHER
Woods Hole Oceanographic Institution

AND

DANA D. KRAMER
Cornell University

Iron in the sea may exist in many physical and chemical forms of which the respective concentrations and availability to microorganisms are not well understood. There appears to be very little present in true solution in seawater (Cooper 1937) and that amount is believed to be insufficient to support phytoplankton at their normal concentrations (Harvey 1937). However, Harvey, and Goldberg (1952) and others have presented evidence that the algae can and do utilize particulate iron as their major source of this element, presumably by hydrolyzing particles adsorbed to their surfaces.

Regardless of the forms in which it exists and may be used, there is frequently very little iron of any kind in the open sea. Total concentrations normally range between 0 and 10 μg/L, about one-half of which will pass through a molecular filter (Lewis and Goldberg 1954, Shaeffer and Bishop 1958, Menzel, unpublished). For convenience, the fractions separated by such filtration techniques have been referred to as "particulate" and "dissolved" iron.

Gran (1933) was among the first to demonstrate that the addition of iron to seawater may stimulate the growth of phytoplankton. Since then many workers have proposed that iron may, at times, limit plant growth in the sea. Recent experiments by Menzel and Ryther (1961) have shown rather conclusively that iron is the most critical nutrient limiting primary production in the tropical and semi-tropical Western Atlantic.

Since iron is associated with land drainage, it is normally present at higher concentrations in coastal waters than in the open sea (cf. Schaeffer and Bishop, loc. cit.). The two regions therefore represent rather different chemical environments (in this and other respects) which could not only affect the general level of productivity but might conceivably provide a selective influence upon the kinds of organisms which could exist and compete with one another under the different conditions. The following experiments were designed to investigate the latter possibility.

Pure cultures of these organisms, listed with the location from which they were isolated, were used in the experiments:

1. *Cyclotella nana* (clone 13-1)	Atlantic Ocean: 33°11′N, 65°15′W
2. *Coccolithus huxleyi*	Atlantic Ocean: 32°10′N, 64°30′W
3. *Chaetoceros lorenzianus*	Atlantic Ocean: 32°10′N, 64°30′W
4. *Chaetoceros* sp. (clone BBSm)	Atlantic Ocean: 32°10′N, 64°30′W
5. *Pyramimonas* sp. (clone 2)	Great South Bay, Long Island, N. Y.
6. *Skeletonema costatum*	Long Island Sound

7. Unidentified cryptomonad (clone 3C)	Long Island Sound
8. *Amphidinium carteri*	Great Pond, Falmouth, Mass.
9. *Isochyris galbana*	Fish pond, Marine Biological Station, Port Erin

These organisms are maintained in pure culture at the Woods Hole Oceanographic Institution. They were all isolated by Dr. R. R. L. Guillard except for *Isochrysis galbana,* isolated and described by Dr. Mary Parke (Parke 1949). Species 1-4 may be considered and will be hereafter referred to as oceanic species, species 5-9 as coastal species.

The organisms are routinely grown at Woods Hole in an enriched seawater designated as medium "f" and consisting of the following addition to millipore-filtered seawater:

$NaNO_3$	150.0 mg/L
$NaHPO_4 \cdot H_2O$	10.0 mg/L
$Na_2SiO_3 \cdot 9H_2O$	30.0 mg/L
Fe-EDTA	10.0 mg/L
Thiamin·HCl	0.2 mg/L
Biotin	1.0 µg/L
B_{12}	1.0 µg/L
$CuSO_4 \cdot 5H_2O$	19.6 µg/L
$ZnSO_4 \cdot 7H_2O$	44.0 µg/L
$CoCl_2 \cdot 6H_2O$	22.0 µg/L
$MnCl_2 \cdot 4H_2O$	360.0 µg/L
$Na_2moO_4 \cdot 2H_2O$	30.0 µg/L

Fe-EDTA is the tetra-valent iron complex of ethylenediamine tetra-acetic acid.

For the experiments to determine iron requirement the organisms were inoculated into medium "f" minus its iron constituent and made from millipore-filtered offshore seawater. After one or 2 transfers through this medium, all the algae with one exception were obviously iron-limited and had ceased growing. The deficient cultures were then inoculated into a series of 50-ml cultures consisting of the same basic medium but enriched with varying concentrations of Fe-EDTA ranging in most cases from 0 to 130 µg Fe/L, but for the crytomonad, 0 to 260 ug/L, and for *Pyramimonas,* 0-1300 µg/L. The one organism which did not obviously develop an iron deficiency, *Coccolithus huxleyi,* was sub-cultured 6 times in the "f minus Fe" medium and then inoculated into the same series of media.

The cultures were grown at 20°C at approximately 1000 ft-c of light until their maximum population density was attained, a period which varied somewhat but ranged from 5-10 days. The population density was then estimated by cell counts with a hemocytometer, by optical density measurements at 750 mµ in a Beckman DU spectrophotometer and by chlorophyll *a* concentrations as determined by spectrophotometric measurements of acetone extracts following the method of Richards with Thompson (1952). Of the 3 methods, cell counts gave by far the most reproducible and interpretable results, despite some variability of cell size at different iron concentrations. These are the only data which will be reported here. In comparing cell counts with chlorophyll concentrations, an obvious increase was observed in the chlorophyll/cell value at successively higher levels of iron as has been reported elsewhere (cf. Fleischer 1935). There were indications that this value varied by more than an order of magnitude in some species, but the chlorophyll data were not sufficiently reliable to show this clearly.

The results of these experiments are reported as a series of curves typical of the "dose-response" curves employed in bioassay work. No attempt was made to define the concentrations of iron available to the organisms at any time. The data thus reflect the response of the algae to the amount of iron available, not to its instantaneous concentration. Even here, the quantity of iron available in the filtered seawater used as a base for the medium is not known, though it was below the level detectable by the ∝, ∝-bipyridyl method of Lewis and Goldberg (1954) and hence may be presumed to have been less than 5 µg/L. For these reasons, the exact iron requirement per cell of the respective organisms cannot be determined from our data with sufficient precision to warrant the attempt. However, the relative requirements of the oceanic and coastal species, as revealed by characteristic features of the dose-response curves, are of considerable ecological significance (Fig. 1).

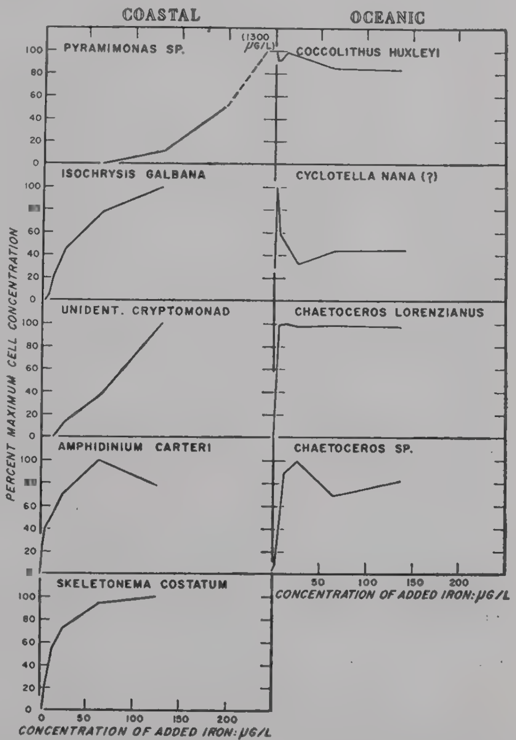

Fig. 1. Terminal population of algae attained in media enriched with various amounts of iron as Fe-EDTA, shown as percentage of maximum population developed for each organism.

Of the oceanic species, *Coccolithus huxleyi* could not be made to show an iron deficiency. After 6 transfers through Fe-deficient media and subsequent inoculation into the graded iron series, the greatest population (3×10^6 cells/ml) still developed in the control culture with no added iron. Apparently the iron originally present in the seawater was adequate for this growth.

All other species tested, once iron-deficient, showed no measurable growth in the control cultures containing no added iron. However, the 3 other oceanic species attained their maximum growth with 2.6 (*Cyclotella nana*), 6.5 (*Chaetoceros lorenzianus*) and 13-26 (*Chaetoceros* sp.) µg/Liter of iron respectively.

Of the coastal species 4 out of 5 failed to grow below 6.5 µg/L, the crytomonad did not increase significantly below 26 µg/L, and *Pyraminonas* sp. required at least 130 µg/L to initiate cell division. The maximum population densities were attained in iron levels of 65 µg/L for *Amphidinium carteri,* 130 µg/L for *Isochrysis galbana*, *Skeletonema costatum* and the crytomonad, and 1300 µg/L for *Pyramimonas* sp. Maximum populations of *Isochrysis*, *Skeletonema* and *Pyramimonas* were attained at the highest level of iron used, at which point growth may still have been iron limited.

We have defined the algae used in these experiments as "coastal" and "oceanic" on the basis of the regions from which they were isolated. We believe that the distinction may go beyond this, and that there are many species, perhaps including some of those tested here, which are restricted in their distribution to one or the other environment. For example, we have found *C. huxleyi* widespread in the open waters of the western Atlantic and the dominant organism during most of the year in the Sargasso Sea near Bermuda (Hulburt *et al.* 1960). Yet it is seldom encountered within the continental shelf waters off eastern United States and never in the shallow coastal waters. Other clones of *C. huxleyi* have been isolated from inshore northern waters (Mjaaland 1956), but that author points out that the species originally described by Lohmann (as *Pontosphaera huxleyi*) represents several taxonomic units. It is doubtful that the Woods Hole clone bears a close relationship, systematically or physiologically, to the forms with which Mjaaland worked, though this should be investigated.

Skeletonema costatum, on the other hand, is a ubiquitous diatom in estuaries and coastal waters throughout the world. It has seldom been reported in the open sea far from land and is probably always of neritic origin. It is significant in relation to these distributional patterns, that *Skeletonema* does not begin to grow at levels of iron which are sufficient to produce populations of *C. huxleyi* orders of magnitude greater than ever encountered in the sea.

Although the number of species used in our experiments was not large, the consistency of the results strongly indictates a general pattern of response. It is not unlikely that coastal and offshore species may respond differentially to the levels of other nutrients, but on the basis of our experiments and the little known of its distribution, iron appears to be one of the more likely factors controlling the distribution of plants in the sea.

SUMMARY

The relative iron requirement of 5 coastal and 4 oceanic species of plankton algae was determined by assaying the growth of iron-deficient cultures in media containing various amounts of Fe-EDTA. The oceanic species attained their maximum populations at levels of iron capable of supporting either no growth or a small fraction of the potential growth of the coastal species under the conditions of the experiment. It is suggested that the availability of iron may be a factor controlling the distribution of these and other species of marine phytoplankton in view of the association of this element with land drainage and its greater abundance in neritic waters.

REFERENCES

Cooper, L. H. N. 1937. Some conditions governing the solubility of iron. Proc. Roy. Soc. **124**: 299-307.

Fleischer, W. E. 1935. The relation between chlorophyll content and the rate of photosynthesis. J. Gen. Physiol. **18**: 573-597.

Goldberg, E. D. 1952. Iron assimilation by marine diatoms. Biol. Bull. **102**: 243-248.

Gran, H. H. 1933. Studies on the biology and chemistry of the Gulf of Maine. II. Distribution of the phytoplankton in August, 1932. Biol. Bull. **64**: 159-181.

Harvey, H. W. 1937. The supply of iron to diatoms. J. Mar. Biol. Ass. U. K. **22**: 205-219.

Hulburt, E. M., J. H. Ryther and R. R. L. Guillard. 1960. The phytoplankton of the Sargasso Sea off Bermuda. J. Cons. int. Explor. Mer. **25**: 115-128.

Lewis, G. L. Jr. and E. D. Goldberg. 1954. Iron in marine waters. J. Marine Res. **13**: 183-197.

Mjaaland, G. 1956. Some laboratory experiments on the coccolithophorid *Coccolithus huxleyi*. Oikos **7**: 251-255.

Menzel, D. W. and J. H. Ryther. 1961. Nutrients limiting the production of phytoplankton in the Sargasso Sea, with special reference to iron. Deep-Sea Res. 7.

Parke, Mary. 1949. Studies on marine flagellates. J. Mar. Biol. Ass. U.K. **28**: 255-286.

Richards, F. A. with T. G. Thompson. 1952. The estimation and characterization of plankton populations by pigment analysis. II. A spectro photometric method for the estimation of plankton pigments. J. Mar. Res. **11**: 156-172.

Schaeffer, M. B. and Y. M. M. Bishop. 1958. Particulate iron in the off-shore waters of the Panama Bight and in the Gulf of Panama. Limnology and Oceanog. **3**: 137-149.

Contribution No. 1177 from the Woods Hole Oceanographic Institution, with the partial support of Research Grant 10693 from the National Science Foundation.

PLANT PHYSIOLOGY: WATER AND SOLUTES[1]

The review of this volume raises anew the questions of the role of physiology and ecology in a day when the majority of titles in the journal PLANT PHYSIOLOGY may seem to be biochemical, and ECOLOGY receives and publishes papers which at an earlier date would have been more characteristic of PLANT PHYSIOLOGY. For those who care less about subject matter distinctions than about the value of a book for enriching their understanding and for developing new viewpoints, this volume offers much to the ecologist interested in studying the plant in relation to its environment. One concept which is alive through its pages is that each plant is a marvelous, vital organism. An infusion of this thinking may not be out of place to counterbalance ecological studies in which the individual plant is reduced to a cipher in a set of ruthless statistical manipulations, or to a docile role in a generalized scheme of plant and environmental relationships. A further tribute to the book is that it is eminently readable throughout. The presentations are relatively non-technical in view of the complexities of several of the topics, which are at the same time rather fully discussed.

Professor Steward in the plan of the treatise points out that the need for and the utilization of inorganic nutrients are to be dealt with in Volume III. The processes of organic nutrition are considered in Volume IV. In the present volume the underlying theme is the basis of plant physiology in cell physiology. Of the 8 contributors, half are from abroad with 3 from Great Britain and Runar Collander from Finland. All of the contributions are well written and edited, and the volume as a whole represents an excellent level of the publisher's art. There are numerous effective illustrations and extensive literature citations. I feel that Fig. 20 in Chap. 7 should more properly have been credited to C. H. Wadleigh and A. D. Ayers.

R. Collander discusses "Cell Membranes: Their Resistance to Penetration and their Capacity for Transport" with emphasis on the substances and factors involved in permeability. He also points out that impermeability is of great importance, and worthy of more study, by isolating the living machinery of the cell from the great diversity of environments in which cells are found.

T. A. Bennet-Clark discusses "Water Relations of Cells" in a highly interesting and stimulating fashion. I recommend this chapter for a possible new viewpoint to persons investigating ecological problems involving water relations. O. V. S. Heath presents "The Water Relations of Stomatal Cells and the Mechanisms of Stomatal Movement." The emphasis is on experimentation and he concludes that, "Stomata seem to provide another example of the tendency found in many living organisms for a single system to be operated by a number of mechanisms which interact in an elaborate way to provide a sensitive control well adapted to the conditions normally encountered."

F. C. Steward and J. F. Sutcliffe devote 225 pages to "Plants in Relation to Inorganic Salts." Among the offerings of particular interest to ecologists are such topics as the composition of the media from which plant cells accumulate solutes, absorption by aerial shoots, the relationships of mycorrhizal fungi, aquatic angiosperms, and excretion and exclusion of salts. C. A. Swanson in "Translocation of Organic Solutes" points out that one melon in growing to a dry weight of 5 pounds or more within a month from the time of pollination has translocated to it the equivalent of approximately 4.5×10^{24} sucrose molecules, which number placed end to end would extend for a distance of about 2½ trillion miles. When we think of the growth and productivity of a complex forest or grassland community, our interest in and respect for understanding of the job done by the phloem and other tissues which may be involved in translocation, and of the influence of environmental factors on their functioning, is greatly enhanced. O. Biddulph considers "Translocation of Inorganic Solutes." Ecological aspects of plant nutrition are influenced by considerations such as that, "90% of the final total of nitrogen and phosphorus taken in by the developing cereal plant was absorbed by the time the dry weight constituted 25% of the final value." Much of the chapter deals with utilization and mobilization of nutrients, related to external supply, internal demand, and morphological relationships. In oats, "93% of the inflorescence phosphorus was derived from other plant parts when excessive external supply was available, whereas in phosphorus-deficient plants only 30% was from other plant parts." Such factors may be important in the irregularity of seed production by many tree species such as beech.

P. J. Kramer discusses "Transpiration and the Water Economy of Plants," a topic which is recognized as of importance by ecologists. Nuggets of ecological interest are found in numerous topics. One paragraph mentions relatively recent work on relating evapotranspiration from land areas to available energy. This type of study offers much of value to ecologists. Dr. Kramer points out the lack of a universally satisfactory time for determining, and basis for calculating, water content, and the need for investigators to be aware of the shortcomings of the methods which they use.

Professor Steward's organizing and editing of the present series is a major contribution to overcoming the difficulties in keeping abreast of current knowledge in the several fields of plant physiology. It was gratifying to note the attention paid to the morphology and organization of the plants and plant systems whose physiological processes were being discussed. The effort taken to secure the precise identification of the species and the plant materials reported upon, and to include the scientific name whenever possible, was highly commendable.

WILLIAM C. ASHBY

DEPARTMENT OF BOTANY
SOUTHERN ILLINOIS UNIVERSITY, CARBONDALE

---

[1] Steward, F. C. (editor). 1959. Plant physiology; a treatise. Vol. II: Plants in relation to water and solutes. (Symposium) Academic Press, New York and London. xvii + 758 pp., figs. and tables. $22.00.

THE PHYSIOLOGY OF TREES[1]

A comprehensive text dealing with the physiology of trees is now available to the botanist, the forester, the horticulturist, and others interested in woody plants. The need for such a book can readily be appreciated when one realizes that the only volume published in English in this field since the 1931 printing of Büsgen and Münch's THE STRUCTURE AND LIFE OF FOREST TREES was the proceedings of the first international symposium on THE PHYSIOLOGY OF FOREST TREES edited by Thimann (1958). As valuable as a collection of papers of this kind is, it cannot be a substitute for an integrated treatise such as the present one.

The 642-page text deals successively with growth and structure, photosynthesis, carbohydrate metabolism, nitrogen relations, fats and related substances, assimilation and respiration, translocation and accumulation, absorption of water and ascent of sap, internal water relations, reproduction, physiology of seeds and seed germination, internal and environmental factors affecting growth.

There is an extensive, up-to-date bibliography of more than 1700 titles including several references to Russian literature. The illustrative material is abundant and well-chosen.

Being of the opinion that tree physiology should deal with individual trees and stands of trees as well as with their processes, the authors have used the ecological approach: physiological processes as a whole are discussed, as well as how they are affected by environmental and internal conditions, while less emphasis is placed on their mechanisms. For detailed treatments of the latter, the reader is referred to standard texts of plant physiology. Such a procedure can be defended on the grounds that the physics and chemistry of physiological processes are essentially the same in trees as in other members of the plant kingdom. The authors could, however, have been more consistent with regard to this point by explaining the mechanism of each major process with the same degree of detail instead of, for instance, enumerating the principal steps in glycolysis and in the Krebs cycle while omitting practically all the intermediate steps of photosynthesis.

One might wish that subject matter had been arranged somewhat differently in a few instances. Growth, for example, is discussed with structure in Chapter 2, and then again in Chapters 15 and 16, which cover the effect of internal and environmental factors on the process. This does not facilitate using the book as a reference. Similarly it might have been more appropriate to have the extensive discussion of water relations precede such topics as translocation and salt absorption.

These are of course minor points when weighed against the wealth of information that has been expertly assembled and digested. The book ably summarizes the state of knowledge in an area of plant physiology that has been rather neglected until recently. It indicates what is yet to be learned in the field, which is considerable, and should thus stimulate further research. It will be extremely valuable as a text and as a reference.

PHILIPPE BOURDEAU
SCHOOL OF FORESTRY
YALE UNIVERSITY

---

[1] Kramer, Paul J. and Theodore T. Kozlowski. 1960. Physiology of trees. McGraw-Hill Book Company, Inc., New York, Toronto, London. xiii + 642 pp. illus. $12.50.

BIOLOGY OF LOBLOLLY PINE[1]

As is indicated by its sub-title, this book on loblolly pine is a comprehensive monograph which summarizes the considerable knowledge of the species and its management "from seedlings to saw logs." It was written by a forester, for foresters, but the silvical treatment in itself, as well as the silvical background for management practices, makes this presentation a reference volume to which ecologists must inevitably turn if in any way interested in the species.

For an ecologist to attempt a detailed or technical appraisal of such a book would be inappropriate. In fact, such a review would probably be out of place in this journal. Suffice it to say then, that here is a volume which has many potential users among ecologists who are hereby being informed of its nature and availability.

The author's objectives were to collect and summarize available information based on research or practice, to organize it systematically, and to evaluate, interpret, illustrate, and report it clearly. Judging primarily from the ecological material, these ends have been admirably accomplished. From the introductory section on resource maintenance and forest history to the conclusion on properties and uses, the presentation is orderly, clear, and readable. Yet, documentation is surprisingly complete and the major results of supporting research are invariably smoothly incorporated. Evidence of the painstaking search for the literature that relates to loblolly pine and the degree of its incorporation in this presentation is a bibliography of over 1600 references.

Adding further to the usefulness of this volume for reference by ecologists is an appendix including various mensurational tables and a list of insects which attack loblolly. Finally, there is a complete author's index and an extensive subject index.

HENRY J. OOSTING
DUKE UNIVERSITY
DURHAM, NORTH CAROLINA

---

[1] Wahlenberg, W. G. 1960. Loblolly pine; its use, ecology, regeneration, protection, growth and management. School of Forestry, Duke University, Durham, N. Car. 603 pp., 79 tables, 116 figs. $7.00.

Soils and Sitka Spruce Forests in British Columbia[1]

This is an ecological study of sitka spruce (*Picea sitchensis*) forests on a variety of topographically different sites in two climatically different parts of coastal British Columbia. The author is a forest pathologist. The study was intended to provide data of potential usefulness in managing sitka spruce as an exotic, planted forest tree in Great Britain. Field work extended over only one season, but a very interesting and valuable study has resulted.

The sites investigated were on the oceanic Queen Charlotte Islands, and a short distance inland on the mainland on the Skeena River where the climate was some 10°F higher at maximum and 10° lower at minimum than on the islands. Soil types, correlations of wet and dry sites with such soil features as texture and such terrain features as river gravel terraces or clay flats, and the suites of species available to form the forests differ in the two areas. However, the ecosystems concerned overlap in properties, and the author in general treats the sites as continuous variables of soil texture, wetness, mineral nutrients, or floras.

In the main the soils are podsols, and the forests are first generation stands of sitka spruce following fires. Day studied the forests after successional regeneration had occurred, and natural thinning and changes in dominance were the main events in the contemporary lives of the stands. The spruce was competing with western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), lodgepole pine (*Pinus contorta* agg.) on the Queen Charlotte Islands and in addition on the mainland with *Abies amabilis, Populus trichocarpa, P. tremuloides, Alnus rubra,* and *Betula papyrifera occidentalis.*

Besides general observations, the author made measurements of the forest stands (basal areas, heights, and ages of trees), rooting depths, presence of species in shrub and ground vegetation, soil profiles, and ground water depths on numerous plots. Unfortunately types were not abstracted from the plot data so generalization and comparison suffer. The data seem loosely organized.

Results of competition between sitka spruce and hemlock as the principal tree species are shown to be a function of nutrient status of the soil. The spruce requires, and can effectively use, high nutrient levels. If nutrient status is high either because of inherent properties of the soil parent material or because of additions of nutrients by moving ground water, then nitrification is high and the spruce dominates, even on the very wet sites. On the other hand if nitrification rate is low, the spruce gives poorer comparative growth and therefore loses out in competition. The competition results in pathological effects in the losers.

Day brings up some interesting points about tree physiology which are distinctive, not usually mentioned, yet of evident importance. A tree is a large and exceedingly long-lived organism. The conditions for establishment of seedlings are thus frequently different from the conditions under which the mature plants grow, and the tree makes the microclimate for its associates, including its own reproduction. Thus most forest stands experience natural thinning. On a poor soil the old forest must therefore be an open one. In the case of the British Columbia spruce-hemlock forests on poor sites this means an old forest acquires a dense understory of ericaceous shrubs when natural thinning opens the canopy to reduce in spots at least the normally dense shade cast by the dominant trees. The effect of these ericads on the soil is probably not one of enrichment but rather of impoverishment. Finally, an old tree needs a larger soil volume from which to draw nutrients than does a young one. In many of Day's alluvial soils a high water table sharply limits depth of rooting. Lateral spread is limited by the needs of neighboring trees. On this relationship Day blames much of the spike-top physiognomy of these maturing forests. The amount of nutrients per unit volume of soil is the ultimate determining factor in the tree's health since a growing tree's needs are continually increasing. Day believes his trees run out of living space, volume of exploitable soil. Those acquainted with soils data will realize at once how few such data are truly quantitative in this sense.

Day's monograph contributes to the factual data on British Columbia coastal spruce forests, their composition, structure, secular changes, and relationships to environment with particular attention to physical soil properties and associated plants. Theories concerned with development of forest plant communities, the interplay of ecological factors, forest pathology, silvicultural management of forests, and site description are also illuminated.

JACK MAJOR

DEPARTMENT OF BOTANY
UNIVERSITY OF CALIFORNIA, DAVIS

---

[1] Day, W. R. 1957. Sitka spruce in British Columbia, a study in forest relationships. Forestry Commission Bulletin No. 28. Her Majesty's Stationery Office, London. 110 pp., 25 figs., 57 plates, 28 tables. 1£ ($2.80).

A System of Soil Classification[1]

In the growth of a science, levels are reached where old concepts, definitions and classifications need amending to accommodate the new discoveries, new data and new techniques that accumulate. The authors of this book believe that soil science has reached this point, but rather than amend the old, they propose an entirely new system of classification with new concepts and reworked definitions to match it. This "approximation" is the seventh and most elaborate of the classification systems that this staff has proposed since 1951 and the first to be published in book form. The authors express the hope that this is the last tentative system before a final one will be adopted for use by the Department of Agriculture and all experiment stations and state agencies concerned with the Soil Survey of the United States. It can be assumed that the final scheme will resemble this approximation in many respects; for this reason workers in all fields of biology that deal with soil relationships to organisms will want to know the "shape of things to come."

---

[1] Soil Survey Staff, Soil Conservation Service, U. S. Department of Agriculture. 1960. Soil Classification, a Comprehensive System, 7th Approximation. Washington. v + 265 pp., Illus. $2.25.

That the older soil classification systems had a certain subjectivity and lack of precision has been a common observation of many who have worked with them. Perhaps those of us not engaged in soil science had the feeling that the kinds of soils were few and simple by nature, and we were content to use a rather simple classification such as that of Baldwin *et al.*, or Thorp and Smith, which had their origins in the great Russian systems of pedology. At any rate, we were schooled in the idea of climatically controlled soils classified on a genetic basis. This basic assumption is challenged by the present work. The authors maintain that a soil should be classified on the basis of what it is today—not by what it is presumed to have developed from. With less and less of the earth's surface having soils undisturbed by man's activities, this point is becoming self-evident. With this in mind the authors discard the old classification schemes of three Orders (Zonal, Intrazonal and Azonal) and about thirty-six Great Soil Groups, and devise a new one which almost painfully avoids retaining even a single word of the old system. A completely new nomenclature is presented which uses coined names exclusively. This is not merely putting "new wine in old bottles"—the concepts of classification are also new.

In any classification system we first wish to know what we are classifying; that is, the precise entities having a physical or conceptual existence. This present system is presumed to be a classification not of concepts, but of things, for the authors state, "The Soil Individuals are the real things we want to classify into Series and higher categories." This leads to a discussion of the "Soil Individual"; we find it to be a less definite entity than we had hoped. It turns out to be, in fact, a concept. To escape this dilemma, the "Pedon" was devised. The pedon concept now tries to become concrete, but in spite of arbitrary delimitations that are set up, seems somehow to elude materialization. It is somewhat disconcerting at this point to have two soil profiles, one from Belgium and the other from South Australia, introduced to clarify the pedon concept. The impression is given that one must go far afield to find clear-cut examples of a unit that is supposed to be all around us. It is little help to say that "the Soil Individual consists of one or many contiguous pedons bounded on all sides by 'not soil' or pedons of unlike character."

Assuming that an entity, or at least a rather definite concept, has been found which is adaptable to classification, the next task is that of organizing a system of hierarchies and subordinate categories in which to place the Soil Individual. To do this according to the expressed aims of this system (i.e., on the basis of properties rather than genesis) the three Orders of the older systems are replaced by ten new Orders that are based on detailed morphological descriptions of each Order and accompanied by specific soil profiles to illustrate actual soils of the Order. The authors find it necessary to introduce as well a new framework for morphological description, differing completely from the familiar O A B C horizon designations. A soil is divided into (1) the diagnostic surface horizon, the "Epipedon," of which six types are named, (2) diagnostic subsurface horizons, including six types, (3) two kinds of "pans" and (4) four other horizons not restricted to either surface or subsurface parts of the soil. The Orders are further "subdivided into Suborders primarily on the basis of the characteristics that seemed to produce classes with the greatest homogeneity. Only one characteristic, the color associated with wetness, was used to define Suborders in each Order in which it is found." In this way 29 Suborders are established and named. The next subdivision is into Great Groups, each defined "within its suborder, largely on the presence or absence of diagnostic horizons and the arrangement of these horizons." This results in the creation of 105 named groups, with two Orders yet to be subdivided. These are in turn divided into Subgroups, which "can be defined only in terms of reference to the great groups. If we think of a great group as occupying a segment of the spectrum of soil properties, the core, or central part of that area is one subgroup. The fringes, where the properties of one great group merge with those of others . . . are intergrade subgroups." There are approximately 349 Subgroups named and described. New taxonomic words and word combinations thus total approximately 493, which, with the new words used in morphological description, brings the total to over 500 new terms. Each of these terms is a coined one, formed according to an elaborate system presented in the book. Tables of "formative elements," taken from Latin, Greek, German, and nonsense syllables, form the bullion for the coinage. These elements are ingeniously combined according to the classification categories in such a manner that subordinate units are built up of components of higher category names. Thus the classification of a term can be derived from the structure of the term itself. A system of numbering parallels the categories. The resulting terms, while mnemonic and connotative, are often so lacking in euphony that they are almost unpronounceable; the Subgroup names range from the rather pleasant-sounding "orthic cryaquents" through the passable "cumulic haplaltolls" to the almost impossible "umbraqueptic dystrochrepts" and "plintaquultic thermaquods."

The simultaneous presentation of so many new coined terms in support of a classification system is probably without parallel in science. If, as the authors state, it actually reflects the growing precision of the science, it may be viewed as a necessary, if bold, step. Certainly the older systems were lacking in precision, and were in need of a serious re-evaluation. If, in the considered judgment of the soil scientists, there exist 349 reasonably distinct Subgroups of soils, and if naming them and formalizing their descriptions serve a useful purpose in a technical understanding of soils, such a system, however burdensome, is proper. We should remember, however, that the stated objective of the system is to classify "soil individuals"—the system as devised so far has not gone below the Subgroup. The Families and Series are not yet defined and named. If the system proliferates new names in an increasing order as it descends to these lower categories, we may expect many thousands of them in the future.

From the viewpoint of a biologist examining this classification, no particular objection can be made to it. We should find it possible to express our general observations on soils in relation to biota with as much accuracy by using one of the ten Soil Orders proposed here as by using one of the thirty-two Great Soil Groups of the older system. If we wish more differentiation we may determine a Suborder name, and so on to the Soil Series (when the classification is developed) as far as our technical skill and patience permit. We are provided with a system of correlated categories of classification—what we do with it is determined by our need for precision. For the biologist this represents a gain, for we had not previously been furnished such an option.

It would be presumptuous for this reviewer to pass judgment on the technical aspects of this classification. It appears to be boldly conceived, elaborately presented and well supported by many actual soil profiles. Its redefinitions and clarification of O A B C profile terminology appear to be very acceptable and a needed improvement of the old. To add an ecologist's viewpoint, it seems that in soil classification we are dealing with different and recombining factors appearing, when viewed from a broad standpoint, to represent a "continuum." In such a system, the fragmentation of the whole into units becomes, in the lowest divisions, arbitrary and rather subjective. This leads to the speculation that so many named categories (349) in the next higher division above the Family level may not be really necessary. This is, of course, a point often raised concerning biological taxonomy; however our multiplicity of questionable divisions is usually at or below the "species" level. We can express the hope that this new precision in soil classification does not make the work of soil scientists (which has been of such great value to biologists in the past) unintelligible to us in the future. The Staff of the Soil Survey is to be congratulated on the presentation, however tentative, of this monumental work.

HANSFORD T. SHACKLETTE

DEPARTMENT OF BOTANY
UNIVERSITY OF MICHIGAN

ECOLOGY OF SOIL MICROORGANISMS[1]

Published as one of the volumes in the "Biological Sciences" series by the Hutchinson University Library, this volume presents a very concise and comprehensive survey of soil microorganisms, principally bacteria, actinomycetes, fungi, algae, protozoa and nematodes.

The soil, its structure, and its manifestations of different types of parent materials under varying conditions of climate and vegetation are summarized in introducing the habitat of the organisms. A general survey is presented of the different types of soil organisms that can be expected in various soil samples. Techniques for estimating the numbers of organisms in soils are described, and surveyed for their adaptability to different conditions. Methods appropriate to each of the different groups of microorganisms are considered critically. The third chapter ends with a discussion of the varying numbers of organisms present in different types of soils under virgin and cultivated conditions from season to season or even hour to hour.

Although "at present our knowledge of the condition in which most of the micro-organisms exist in the soil is relatively scanty . . . ," Burges has brought together considerable information from work done on fungi, bacteria and nematodes, to show that their activities in natural conditions and in laboratory culture are strongly contrasted. Some fungi are found only as spores, others can be readily observed as mycelia; most bacteria occur as small groups of cells, the mucilaginous exudates of some of which may aid in aggregation of soil particles through cementing activities; and protozoans and nematodes may exist as cysts or active individuals in varying percentages from month to month or season to season.

The distribution of organisms within the soil is an interesting field in which to work. Factors affecting distribution include food supply, carbon dioxide tolerance or oxygen availability, presence of root systems and presence of decomposable substrata. Numbers of fungal colonies in soils normally decrease rapidly downward, but this decrease may be modified somewhat where wettable spores are carried down through sandy soil by percolating waters. Algae are usually restricted to the surface layers of soils. Fungi and bacteria may be present in large numbers in the rhizosphere, and various nutrient groups of these organisms will vary in number of individuals with the age of the plant and even the type of plant producing the particular rhizosphere under consideration.

Many soil organisms complete their life cycle entirely within the soil, others require changes in habitat as the nutrient requirements change for different phases of their life cycle. The ecology of these organisms is highly complex and much information will be needed before this is completely understood. Chapter 6 summarizes what is known of this phase of soil microbiology. The population includes obligate plant or animal parasites, parasites which may be soil invaders or soil inhabitants as well as invaders of moribund tissues, and true soil organisms including the zymogeneous organisms which rapidly utilize the fraction of organic matter available to them, and the autochthonous organisms which are permanent inhabitants of soils and which take longer periods of time to utilize available nutrients. Five groups of bacteria are recognized, each of them finding a different place in the pattern of reduction of organic matter in the soil. Birch and Clarke's ecological grouping of soil organisms based on their feeding habits is presented and analyzed.

The role of microorganisms in the various cycles such as nitrogen, carbon, minerals and sulphur is considered in some detail since it is largely through their activity that these elements are made available to higher plants and animals. In his agricultural practices man affects the microorganisms in the soil in many ways: by upsetting balances of nutrition, thus establishing or promoting the establishment of new populations based on different organisms: by adding poisons to the soil for soil sterilization purposes; by adding other poisons to the soil through attempts at weed control, insect control, or the control of plant disease fungi; by continually growing one crop on the same soil, resulting in exhaustion of that soil or in the phenomenon called "soil sickness"; and by other practices either detrimental to the soil or resulting in apparently favorable attempts to improve the soil.

"The soil like all biological systems undergoes continual change but nevertheless remains comparatively stable." The last chapter brings together much information to show that the soil is a biological system in a state of dynamic equilibrium. Every type of phenomenon observed in systems of populations from symbiosis to parasitism, using these terms in their broadest meaning, is demonstrated by a balanced soil population.

The book is well written, interesting, and is free from typographical error. Its bibliography includes 175 references. For anyone interested in the total ecology of any area this should be a reference book, for whether the soil type of his area is mentioned in it or not, much of the contents will apply to his particular problem. It should be in every ecologist's reference library and available to every student interested in the study and practices of ecology.

WM. BRIDGE COOKE

ROBERT A. TAFT SANITARY ENGINEERING CENTER
CINCINNATI, OHIO

---

[1] Burges, Alan. 1958. Microorganisms in the soil. Hutchinson University Library, London. 188 pp.. 10 s, 6 d, $1.50.

SOIL FUNGUS ECOLOGY[1]

Thirty-five microbiologists, mycologists, soil biologists and applied mycologists met at a University of Liverpool symposium on "The Ecology of Soil Fungi." Representing England, Wales, Scotland, Canada, Australia, New Zealand, Belgium, Germany, France and Poland, these people exchanged experiences and views that are recorded in 28 chapters, 6 sections. Each section ends with the meat of the discussions which followed the oral presentations, often containing as much of interest to the reader as the chapters under consideration.

Starting with descriptions and criticisms of methods for isolation and estimation of activity of fungi in soil, we are taken through chapters on the growth of fungi in soil, antagonisms in soil, dynamic equilibria of soil populations, problems associated with the decomposition of organic matter in soils, and finally problems in the physiology of soil fungi. Some chapters are necessarily reviews of previous work done in the participant's laboratory or in his special realm of activity. Other chapters briefly summarize earlier work but report largely on original research in progress, much of it in uncharted areas of interest.

With the exception of a chapter on the actinomycete causing potato scab, emphasis throughout the book is on the fungi, with occasional reference to other organisms in their environment. In this first collection of reports of research on all phases of the activity of fungi in the soil, one can learn how much or how little is known of such activity, points concerning additional information needed, and trends for additional studies.

Many techniques have been used in assessing the fungal populations of a soil. Dilution techniques result in information concerning those species present as spores; soil plates and hyphal isolation add data concerning activities. Combinations of isolation and direct observation are necessary to develop full information about any population. Estimates of absolute numbers of fungi and relative frequencies of different species present complementary information.

Upon applying different techniques of isolation of fungi from soil, the effects of nutrient supplies and other habitat variables can be assessed. Biotic influences, comparative growth in forest and grassland soils, growth in desert sands, and the effects of mineral fertilizers on soil fungi are considered.

Physical, mechanical and chemical aspects of antagonistic and competitive mechanisms limiting survival and activity of fungi in soils are considered. Some species may produce antibiotics, but whether this ability is as general in the natural soil as in the laboratory is uncertain, and whether these substances are byproducts of metabolism acting against other organisms present is not yet clarified. Certainly there is inhibition of spore germination, developing mycelium, and other growth structures, but its exact nature and degree have still to be described.

Within the soil are many microhabitats, and within each the population is in a dynamic equilibrium: removal or addition of a nutrient may change the habitat, but members of the population are able to adjust to this change. Five major fungal population patterns are selected for elaboration. The place of fungi in the rhizosphere is coming to be appreciated from studies in agricultural soils, tidal mud flats, and soils of young forest plantations.

Among the primary agents of the decomposition of organic matter elaborated by green plants, animals of all kinds, and even the fungi themselves, are the fungi which in the soil continually aid in the numerous cycles returning carbon, nitrogen and other elements to forms in which they can again be used by micro- and macroorganisms. Techniques and results of studying these processes in relation to general soil organic matter, humic acids, and buried cellulose film are considered.

The study of physiological processes, largely using biochemical reaction techniques, is described for general soil fungi, and fungi associated in mycorrhizae with various plant roots, as well as the use of tissue preparations in oxidative metabolism studies of Krebs Cycle reactions and the decomposition of lignin. Henderson reports the greatest progress to date in our knowledge of the breakdown by fungi of lignin, lignin building blocks and lignin decomposition products. However, according to Harley, "We have to conclude that the study of the physiology of fungi in culture has outlined the kinds of variability in requirements for essential materials and the kinds of reaction they can bring about, but as yet it has afforded little in explaining in detail their ecological distribution except in a few cases."

The materials compiled in this book and the types of information emphasized as most important seem to this reviewer to point up a major difference between the views of students in Europe and those in North America. At least in the United States the study of soil organisms is largely a study in soils biochemistry: what reaction will take place under one added nutrient or another; what reaction can be hindered by the application of one inhibitor or another?

The book is well written, the style making it easily read. There is a minimum of typographical errors in the main text, but proof-reading of the discussion sections was a trifle hasty. Each chapter is followed by its own bibliography except a few having no reference material, the others listing two to 60 references. Although the study of soil mycology is a very active field, this summary will probably not be matched for a number of years. For those desiring information relative to total productivity of any land surface, this volume will provide an excellent source of information for one important segment of the population. For the ecologists' reference shelf this book can be an important addition, bringing together so much information about the activities of fungi in soils and pointing up study areas where additional information is a necessity.

WM. BRIDGE COOKE
ROBERT A. TAFT SANITARY ENGINEERING CENTER
CINCINNITI, OHIO

---

[1] Parkinson, D. and J. S. Waid (editors) 1960. The ecology of soil fungi, an international symposium. Liverpool University Press, Liverpool. xi + 324 pp., figs. & tables. 42 s. 6d, $6.00.

BACTERIOLOGY OF LAKES[1]

This excellently treats the old "microbiology," which centered on bacteria with only perfunctory attention to algae, and practically none to fungi and protozoa. In the Winogradsky-Waksman-Zobell tradition, emphasis is on the statistical distribution of bacteria in lakes, with some attention to specialists such as sulfate reducers, denitrificers, nitrogen-fixers, and photosynthesizers. The conclusion is reached, as in other books of this kind, that the more food and lodgements, the more bacteria. The ecologist seeking a book to help him understand the succession of forms in nature, or the exact identity of microbes which perform a specialized biochemical function, must go to the original literature or strike out into the unknown for himself: no one book on microbiology will orient him much except for such comprehensive works as Edmondson's 2nd edition of Ward and Whipple's FRESH WATER BIOLOGY.

The difficulty confronting the ecologist needing understanding of a microbial group performing a specialized job is that the literature on identification is very spotty, even for soil bacteria. Little has been done with water bacteria. The present book has few references to work more recent than 1950.

The beginning of an ecologically meaningful fitting together of the activities of different microbial groups is discerned in such studies as those of the Burkholders, who showed that the intense production of vitamins by unidentified bacteria and algae in mangrove mud helped account for the abundance of dinoflagellates in the Phosphorescent Bay of Puerto Rico. Comparable studies of ecologically significant interactions of shore-and-bottom microfloras and lake microfloras are almost completely lacking. If one shares the reviewer's opinion that statistics are the lowest form of information, then books such as Kusnezow's and its English-language counterparts, however conscientiously compiled, deliver far less than they promise in the way of understanding.

S. H. HUTNER

HASKINS LABORATORIES
NEW YORK

---

[1] Kusnezow, S. I. 1959. "Die Rolle der Mikroorganismen im Stoffkrieslauf der Seen." Translated from the Russian by A. Pochmann. VEB Deutscher Verlag der Wissenschaften, (East) Berlin. x + 301 pp., 77 figs. DM 36,—, $8.60.

THE INTERNAL ENVIRONMENT OF CRUSTACEA[1]

Claude Bernard's famous and oft-quoted aphorism concerning the relationship of the *mileu intérieur* to the *milieu extérieur* is recalled once again by the appearance of this first volume of a planned two-volume work on the comparative physiology of the Crustacea. Edited, and written in part, by Talbot H. Waterman, the book is divided into seventeen chapters dealing with aspects of growth and metabolism. The individual chapters are: General crustacean biology by T. H. Waterman and F. A. Chace, Jr., Respiration by H. P. Wolvekamp, Biochemistry of pigments by T. W. Goodwin, Blood chemistry by M. Florkin, Circulation and heart function by D. M. Maynard, Feeding and nutrition by S. M. Marshall and A. P. Orr, Vitamins by L. R. Fisher, Digestion and metabolism by H. J. Vonk, Osmotic and ionic regulation by J. D. Robertson, Excretion by G. Parry, Terrestrial adaptations by E. B. Edney, Ecology and metabolism by M. Florkin, Sex determination by H. Charmiaux-Cotton, Integument and exoskeleton by R. Dennell, Molting and its control by L. M. Passano, Relative growth by G. Teissier, Autontomy and regeneration by D. E. Bliss. Despite the comprehensive nature of the contributions, each naturally reflects the enthusiasms and preoccupations of the author.

Many ecologists are studying crustaceans and rely heavily on a physiological approach. What is there of ecological interest in this volume? There is a great deal, but finding it may require considerable digging. Almost all of the writing has a biochemical orientation, no bad thing in itself. But the ecologist will not have all the possible implications pointed out and underscored. Specific references to ecology are made in Chapters 1, 11, and 12.

The first chapter, on general crustacean biology, is an adequate and unpretentious once-over-lightly presentation on morphology, systematics, evolution and embryology. Ecology is given a separate section but the treatment is too general to justify its inclusion. The chapter is most interesting where it gives some indication of recent thinking concerning evolution within the class. An expanded coverage of the characteristics and phylogenetic relationships of each of the sub-classes would have been useful for reference when reading the subsequent chapters.

The chapter on respiration ends with the statement that the crustacea do not seem to differ significantly from other invertebrates in their respiratory functions and the exhaustive consideration of the data seems to prove it. It would have been better to have condensed this discussion and to have included most of the material on intermediary metabolism found in other chapters, since oxygen assimilation is only a means to an end.

The chapter on feeding and nutrition will be of some interest, perhaps especially because the shock of finding almost no quantitative data should prove stimulating. Indeed, we are in the unenviable position of not knowing what most crustaceans eat.

Under terrestrial adaptations are discussed adaptation to temperature and moisture regimes of dry land. Since most crustaceans are aquatic, their existence on land is marginal at best and only one suborder is completely terrestrial. Unfortunately, problems of water conservation, respiration, locomotion and mating are discussed in the most general terms. The occupation of unique terrestrial habitats such as caves, burrows, trees, etc., is regarded as "outside the scope of the chapter."

Only one other *caveat* will be mentioned. Ecologists very likely will turn at once to the chapter labeled Ecology and Metabolism, to be greatly disappointed. The chapter is mostly a rehash of material on temperature responses, respiration and osmotic stress, discussed at greater length in other parts of the book. Special environments *do* come within the scope of this chapter, but only cave dwellers and deep sea forms are covered, and these in very summary fashion. This type of material plus that on the metabolic effects of parasitation could have been explored in much greater detail. As it is, the chapter merely whets the appetite.

---

[1] Waterman, Talbot H. (editor). 1960. The physiology of crustacea. Vol. 1: Metabolism and growth. (symposium) Academic Press Inc., New York & London. xvii + 670 pp., figs. & tables. $22.00.

The pros and cons of "symposium" reviews have been discussed at length many times before. The present work combines the usual advantages and disadvantages of its format. Obviously one person no longer can have a complete working knowledge of the biology of an entire class of animals. Multiple authorship is a logical solution. However, assigning each chapter to a separate author invites some redundancy and omissions which even the most authoritative and hard-working editor cannot hope to avoid.

The special merit of this volume is that it provides an enormous amount of well-digested information about the Crustacea, particularly in areas not frequently included in review articles, in a succinct, even-handed, and relatively well-integrated manner. Certainly, in style, content, and purpose, the individual chapters show much greater consistency than is usually found in such works. The subject, author, and systematic indices are marvels of thoroughness and usefulness. Hopes of widespread ownership of this work will be partially vitiated by its price.

Herbert Curl, Jr.

Woods Hole Oceanographic Institution

F. S. Bodenheimer—Pioneer Ecologist[1]

Frederick Simon Bodenheimer published in the year of his death an autobiography which tells the story of both his personal life and his professional career in biology. The autobiography, subtitled "A Book of Reminiscences," describes his scientific training, foreign travel, teaching, research, and publications in the fields of agricultural entomology, Israel fauna, animal ecology, and the history of biology. He was born and educated in Germany, receiving his doctorate in zoology in 1921. The following year he went to Palestine where he was head of the Department of Entomology at the Agricultural Experimental Station for six years. From 1928 to 1953, he was first a Research Fellow and later a Professor of Zoology at the Hebrew University, where his studies and teaching were in the field of general zoology, ecology, and entomology. He was at the time of his death Emeritus Professor of Zoology at this University in Jerusalem. Throughout his life he devoted himself to the development of economic entomology, faunistic zoology, animal ecology, and the history of biology of Palestine in particular, and over a world-wide scale in general. In spite of seven years spent in active military service, and six years lost to productive work because of illness, Dr. Bodenheimer produced a total of 420 publications between 1919 and 1959. Four additional contributions are now in press.

His life and autobiography both center around his scientific studies. His work began at a time when the foundations of modern animal ecology were just being laid. He became the pioneer and most noted animal ecologist in the Middle East. As a young student he had been influenced by Haeckel's Natural History of Creation. As a youth he was fascinated by observations on animal life, although oddly enough, he was not attracted to the insects at that time. Later, the insects became his primary taxonomic interest and the principle tool of his studies in animal ecology. He also fell under the influence of Richard Hesse to whom he owed, "My introduction to the problems of animal ecology."

Upon his arrival in Tel-Aviv in 1922, he not only had charge of the work in economic entomology for the Agricultural Experimental Station, but he later organized the teaching of this subject in the Hebrew University. At that time, "knowledge of the country, its ecology and its agriculture, its climate, vegetation, and fauna was rather vague." When he first arrived in Palestine, he worked under most trying conditions and with very meager equipment. He described the situation as follows: "I had brought a microscope with me. In Tel-Aviv I secured a room, a table, two chairs, a stand with twenty empty jelly-jars for breeding, a monthly budget of one pound, and nothing more. I received my first salary seven and a half months after arrival. Such were conditions at that time, but we did not grumble but fell to our work with ardor."

After 35 years of service, he was given a banquet on his 60th birthday at which time he claimed that "ecology is the background of the most vital problems of our time, the key to the future of humanity," and stated his conviction that the "future of agriculture in the widest sense does not depend upon better methods of exploitation and production, but upon a radical change in the mentality of those who plan agriculture, in a revolutionary change from reckless utilitarianism to ecological thinking." For the Committee on the Cultural History of Mankind, sponsored by UNESCO, he also stated his philosophy that "it's only the ecologist who can really and truly weigh and estimate all expert opinions and gauge their intrinsic value with our environment, its production and its equilibrium. This is the task and the value of ecological planning in all fields of production: agriculture, industry, human settlement, human health, and preventive medicine."

Dr. Bodenheimer's personal research centered largely around citrus insects, locusts, aphids, scale insects, and voles. He published in German, Hebrew, English, and French. His principle works in ecology are the books entitled Problems of Animal Ecology (1938), Problems of Vole Populations in the Middle East (1949), Insects as Human Food (1951), Prècis d'Ecologie Animale (1954), The Ecology and Taxonomy of the Aphidoidea of the Middle East (1957), and Animal Ecology Today (1958). The book gives the background of each study, and the problems involved. His most regrettable experiences were the necessity of having the manuscript of one book buried in Amsterdam for the duration of the Nazi occupation and the destruction of available copies of another book by the Nazis. He made lasting contributions to the study of insect diapause, animal and human populations, desert ecology, and synecology. One of his best known contributions was the development of the hyberbola curve for predicting insect development.

---

[1] Bodenheimer, F. S. 1959. A biologist in Israel. Biological Studies, Publishers, P.O. Box 1174, Jerusalem, Israel. 492 pp., 45 plates, and 99 Figs.

His working philosophy developed from his researches is scattered throughout the book. For example, from his studies on aphids he concluded, "there is no easy and dogmatic solution for any problem," and from his work on scale insects he was convinced that, "It is essential that every zoologist—and certainly every ecologist—acquire good knowledge of some special animal group, no matter how small." From his work on honey bees he learned that, "the more we know about an animal, the more important new aspects turn up." Experiments with voles cautioned him that, "No conclusions concerning behavior in nature can be drawn from that in experimental cages." Some general conclusions arising from his study of ecology are stated thus, "The life history of the individual species will always remain the basis of animal ecology" and "There are more scientific roads to knowledge than one. Scientific induction gives us well measured and secured facts. The theories which are the soul of science are, however, secured by intuition and deduction. Both roads are admissible and of basic value."

Considering the times and the conditions in which he lived, the years he gave to military service and political activity, and time lost to illness, it is amazing he was able to accomplish as much as he did, attaining international recognition in three major fields of scholarship—agricultural entomology, animal ecology, and history of biology.

RALPH W. DEXTER

DEPARTMENT OF BIOLOGY
KENT STATE UNIVERSITY
KENT, OHIO

A REFERENCE TEXT ON CONSERVATION[1]

Professor Smith and his colleagues have performed a valuable service to students of conservation by bringing out this second edition of the widely used text originally published in 1950. Nineteen authors have contributed twenty-three chapters, the editor being responsible for five himself. The inevitable unevenness and lack of continuity which results from this type of treatment is at least partly offset by the greater depth which many of the authors contribute to their sections, on subjects in which they are well known authorities.

The eight parts into which the book is arranged are concerned with history and economics, soil, forests, water, minerals, fish and wildlife, and the two final parts on human resources and planning. Each chapter concludes with a list of selected references, which are useful and brought reasonably up to date. The book is profusely illustrated with photographs, graphs, and maps which are generally effective.

It is the impression of this reader that the book will be more effective as a reference work, and for assigned readings of individual chapters, than as a regular text for the college courses for which it was intended. Most of the chapters are relatively difficult reading, because of the authors' inclination to pack as much as possible of their fields of specialization into a relatively small space. The treatment is thus heavily factual and statistical, and to a considerable extent historical, so that the important principles do not stand out as effectively as in some of the other contemporary texts.

The sections on forests and on fish and wildlife would be of special interest to the readers of ECOLOGY. The former was improved by deletion of the chapter on "tree crops" which had appeared in the first edition, but still seems to me both weak and disproportionately brief when one considers the importance of forestry in the conservation movement in this country. Matters of public policy, so important in the forestry field, are touched only very lightly, and the role of the federal and state forest services is scarcely mentioned. Its selected references are not as useful as those following most chapters. The chapters on wildlife by Charles Dambach and fisheries by Howard Martin are handled well.

Among the features which contribute to the value of this work as a reference or collateral reading in conservation teaching are the lists of selected references and the exceptionally detailed and useful index. It is a valuable contribution to the literature of conservation in the United States.

GUSTAV A. SWANSON

DEPARTMENT OF CONSERVATION
CORNELL UNIVERSITY

[1] Smith, Guy-Harold (editor) 1958. Conservation of natural resources. Second edition. (symposium) John Wiley & Sons, Inc., New York; Chapman & Hall, Ltd., London. xi + 474 pp., figs. & tables. $8.50.

ECOLOGY AND WILDERNESS[1]

This handsome book records some ideas and experiences in the study of ecology in nature's laboratories and museums by 7 distinguished professional ecologists. It has a thoughtful summary foreword by Brower, a welcome by the president of the Sierra Club, Dr. H. C. Bradley, recommendations by the Conference, and a pertinent postscript. The last is a reprint of a lecture by G. M. Trevelyan delivered in London in 1931 on "The Call and Claims of Natural Beauty."

Trevelyan as a humanist equated nature and beauty. This is not only a most sad idea for humanity in general but a highly relevant one for a wilderness conference, even though added as a postcript to this one.

Dr. Bradley mentioned that "because we love (this

[1] Brower, David (editor) 1960. The meaning of wilderness to science; Proceedings of the 6th Biennial Wilderness Conference, San Francisco 20-21 March 1959. Sierra Club, San Francisco. xi + 130 pp., photographs. $5.75.

wilderness environment), we instinctively seek to understand and to preserve it." Many ecologists might argue that the causation is reversed. At any rate, this theme of understanding wilderness for the scientist's benefit, as well as for his science's benefit, was the theme of the conference.

But surely ecologists are members of that modern genus, Economic man, so why should they exhibit the bias for work in wilderness that they do in fact exhibit? This bias is often a cause for wonder among applied ecologists, among foresters, range managers, agronomists, weed control specialists, hydrologists, wildlife managers, and animal husbandmen. The answer is quite simple and eminently rational, not necessarily emotional or aesthetic. The ecosystem is a complicated system partly because it is a function of many factors. One way to understand, to solve or analyze, this system is to hold all factors but one constant and study *its* effects. Alternatively one can make sure the effects of all factors but one are negligible. Man's activities is one of the factors that affects ecosystems. Wilderness eliminates civilized man as an ecological factor. The system is thereby simplified for study.

The rest of the factors, of course, define the ecosystem and its state. Thus, neither one-factor ecology as such nor holism as such are complete or useful. The ecosystem must be defined by all its factors or properties, but analysis is possible by isolating single factors and properties. Is analysis possible in *any* other way?

D. B. Beard of the National Park Service in his address on "Plants and animals in natural communities" showed an awareness of the instability of the natural communities found even in wilderness. In the ensuing discussion on "managed wilderness" lack of knowledge of natural communities and the effects on them of fire, animal irruptions, etc. became evident. S. A. Cain took up the subject from there in "Ecological islands as natural laboratories." "The wilderness should be studied to enhance enjoyment—the enjoyment of people who are interested in wilderness, who visit, love, and cherish it." Trevelyan is right. There is an aesthetic appreciation of nature on the part of very many people. And Cain makes the point that basic ecological research is not going on in the National Parks as a National Park Service activity. Cahalane's study at Katmai is excellent, but still a first inventory.

Naturally all wilderness in the United States is not in the National Parks. Most is on federal land simply because, as Beard put it, wilderness has been a place with as yet undiscovered economic value. Administration of this land has been custodial, not active. Usually the establishment of a management policy has meant the destruction of wilderness.

Other land administration agencies besides the Park Service are not studying wilderness ecology. Forest Service research acts as a branch of administration, and the Agricultural Research Service has not yet recognized any responsibilities in the field of research on natural ecosystems. The Geological Survey is quite capable of omitting biology altogether—as in a recent book on the "landscapes" of Alaska. Such an omission requires a most peculiarly narrow and myopic view of the world which will quite incidentally make a garbage dump of a triangulation point.

The Forest Service has been investigating recreational use of at least part of the Sierra Nevada wilderness area. Such use is really outside the scope of the Conference reported here except as it touches Trevelyan's theme. In many foreign countries recreational use of the usual kinds is deemed outside the range of wilderness values altogether. Their limited wilderness areas simply cannot stand what we term "recreational use."

The contrast with ecological research in the Swiss National Park is interesting (cf. ECOLOGY 40(2):330-1, 1959). There biological inventories have been complete and adequate. Now, community and developmental studies are possible. In fact Braun-Blanquet and his collaborators' work on the vegetation and soils of the Swiss National Park in Graubunden has elevated both phytosociology and pedology. It is true that our National Parks run very skillful programs of popular appreciation. However, one misses from them advances in scientific knowledge. Skillful popularization of the wonders of nature can awake and sustain a devotion to our natural scenic treasures; but unless this popularization is based on solid and continuing scientific studies, it degenerates into emotionalism and nature-faking and is then vulnerable to economic reasoning, whether rapacious or not, based on cold facts if not cold cash. Continuing protection of our wilderness is still a problem, and this job would certainly be easier if the public could appreciate it more, could know more about it.

L. B. Leopold talked of "Ecological systems and the water resource" and pointed out that the science of hydrology in general is mixing the influences of natural factors affecting the hydrologic cycle with man's influences. Obviously then "water management" is a misnomer if management implies some measure of intelligent control and ability to predict what will happen.

The other speakers were all zoologists. Robert Rausch spoke on "The outlook for conservation in Alaska." Conclusion: Not good since it interferes with making a fast buck. Rausch gave a valuable summary of current wilderness proposals in Alaska. I. M. Cowan's paper on "Science and the wilderness" was concerned with animal populations under natural conditions. It was slide-illustrated. The printed report is tantalizing without the illustrations. Modern communication techniques available to scientists are utterly incapable of reproducing this kind of slide-illustrated lecture. R. B. Cowles on "Population pressure and natural resources" makes a logical attack on the problem of man's spoliation of the earth—there are too many men. A reasoned solution is not possible under such conditions. As Cowles points out, to appeal to increased industrialization for a *worldwide* solution of the problem is logically ridiculous.

E. F. Darling's talk was on "Wilderness, science, and human ecology." He pointed out that applied ecology in most cases has no base from which to apply. Time's arrow with us astride produces the universality of change, a difference between one state of an ecosystem and a following state. Integration of a differential equation produces an answer in the form of a difference, between one state and another. Darling's point is simply that ecologists have not adequately defined the base states. In this symposium he was joined in this view by at least Cain, Leopold, Rausch, Cowan plus many of the discussants.

The discussions of the papers are printed. As usual they contain little speeches, impertinent questions, tangents, offshoots but also some excellent contributions, additions, explanations. They too, are well worth reading.

The resolutions mention specific wilderness areas as scientific resources, that research in wilderness areas is inadequate, and suggest ways for responsible federal land managing agencies to alleviate pressures for destruction of wilderness.

This is a short book with an important and interesting message for ecologists. Its high cost is offset by a wonderful collection of Alaskan photographs, by the abilities of the speakers and the pertinency of their ideas, by the excellence of the discussions, by Trevelyan's essay, by Brower's comments, and by the importance of the subject to ecologists.

JACK MAJOR

DEPARTMENT OF BOTANY
UNIVERSITY OF CALIFORNIA, DAVIS